

PHYLOGENETIC RELATIONSHIPS IN THE CEPHALOPOD FAMILY CRANCHIIDAE (OEGOPSIDA)

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ABSTRACT

Fourteen qualitative morphological characters of squids of the oegopsid family Cranchiidae are described, and the distribution of their states among thirteen genera tabulated. Primitive and derived conditions for each character are inferred on the basis of outgroup comparisons and analyses of ontogenetic transformation series. Application of a Wagner Tree algorithm and Character Compatibility Analysis to the resulting data matrix yields nearly identical reconstructions of cranchiid phylogeny. Hypotheses of monophyly for the traditional subfamilies Cranchiinae and Taoniinae as well as for two of the three groupings of taoniin genera proposed by N. Voss (1980) are shown to be well corroborated, and refinements of previous ideas about cranchiid relationships are also proposed. Little homoplasy is evident in most of the characters of the study, but the anatomical position of digestive duct appendages appears to possess considerable evolutionary lability. Sources of new data for phylogenetic tests are suggested, and the need for additional research on teuthoid comparative morphology is emphasized.

Key words: Mollusca; Cephalopoda; Cranchiidae; phylogenetic inference; Wagner Tree; Character Compatibility.

INTRODUCTION

Phylogenetic studies of living Cephalopoda are long overdue, but until recently have hardly been possible because of the uncertain taxonomy of many groups and the absence of sufficient comparative anatomical data on which to base reliable estimates of evolutionary relationships (G. Voss, 1977a). Past taxonomic studies have usually emphasized external morphology with only incidental treatment, if any, of internal structures, and the systematic potential of many organ systems has, therefore, seldom been explored. This is unfortunate because it seems desirable that classifications be based on as broad a suite of biological attributes as possible. Additionally, the fossil record of cephalopods, as it relates to the genealogy of most contemporary taxa, is inadequate (Donovan, 1977).

The large and morphologically diverse pelagic squid family Cranchiidae was recently revised by N. Voss (1980). Thirteen valid genera were recognized and were arranged into two subfamilies, the Cranchiinae with three constituent genera (*Cranchia*, *Lio-cranchia* and *Leachia*), and the Taoniinae with ten (*Helicocranchia*, *Bathothetauma*, *Sandalops*, *Liguriella*, *Taonius*, *Galiteuthis*,

Mesonychoteuthis, *Egea*, *Megalocranchia* and *Teuthowenia*). Hypotheses of natural generic groupings within the Taoniinae were presented and the taxonomic distribution of a large number of morphological characters was tabulated. The present paper subjects data gathered by N. Voss (1980) on cranchiid comparative morphology to quantitative phylogenetic analysis in order to derive maximally-corroborated hypotheses of relationships for these squids. It is our intention by so doing to test ideas about cranchiid classification presented in the 1980 paper, to argue the utility of much broader surveys of teuthoid morphology than have hitherto been undertaken, and to demonstrate the application of explicitly phylogenetic procedures to systematic studies of contemporary cephalopods.

MATERIALS AND METHODS

The material examined during this study is from the extensive cranchiid collection amassed at the University of Miami over a period of several years from numerous loaning institutions and from the general cephalopod collection of Miami's invertebrate museum, supplemented by the collections of the

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U.S. National Museum. Specimens illustrated in the text belong to the following institutions: Australian Museum (AM), Dominion Museum, New Zealand (DMNZ), Institut Océanographique, Monaco (IOM), Institut für Seefischerei und Zoologisches Museum der Universität Hamburg (ZMH), Newfoundland Biological Station (NBS), Scripps Institution of Oceanography (SIO), South African Museum (SAM), United States National Museum of Natural History (USNM) and the University of Miami Rosenstiel School of Marine and Atmospheric Science (UMML).

1. Character Analysis

This study analyzes the historical information content of 14 qualitative morphological characters and samples variation in anatomical features associated with reproduction, locomotion, feeding, digestion, excretion, structural support and concealment from predators; aspects of both larval and adult morphology are represented. Characters here treated were selected from among those discussed by N. Voss (1980) on the basis of their within-genus constancy and because the variants of the morphological expressions they represent could be coded as discrete states with minimal ambiguity. Character constancy within taxa of low rank seems desirable because such constancy may reflect evolutionary conservatism (Farris, 1966), and choosing characters with easily-described states minimizes the possibility of misclassifying the objects of study. Less rigorous criteria for character choice would have admitted a larger number of characters for phylogenetic analysis but probably at the risk of introducing more homoplasy to the data. The single exception, in this study, to our requirement that character expressions be constant within genera is discussed in the analysis of Character 11, below.

Our arguments for determinations of cranchiid character polarities are presented individually, character by character, but fall broadly into two categories based on the criteria that we used to estimate relative primitiveness. Recent reviews and discussions of methods of polarity estimation are provided by Stevens (1980) and Watrous & Wheeler (1981).

Outgroup comparisons: Of two or more alternative morphological conditions observed among cranchiid squids, the one that also occurs among other teuthoid cephalopods is here hypothesized to be primitive. When two or more states of a cranchiid character whose

polarity was in question were encountered among other teuthoids, however, then polarity estimation required comparisons within yet narrower limits of cranchiid relationships. Choice of a more restricted outgroup was also dictated by the impracticality of tabulating character state distributions for all of the 24 families and 66 genera of living, non-cranchiid teuthoids (see G. Voss, 1977b) when original dissections were necessary to determine anatomical features rarely described or figured in the literature. In the absence of any well-corroborated estimate of teuthoid phylogeny from which an appropriate cranchiid sister group might have been chosen, we restricted our attention, when necessary, to comparisons with only seven other oegopsid families: *Thysanoteuthidae*, *Cycloteuthidae*, *Chiroteuthidae*, *Grimalditeuthidae*, *Mastigoteuthidae*, *Joubiniteuthidae*, and *Promachoteuthidae*. These families share, with cranchiids, 1) a funnel-locking apparatus other than a simple ridge-and-groove, and 2) ventral connectives between the buccal membranes and arms IV (Young & Roper, 1969a, b; Roper *et al.*, 1969). Whether these traits are really synapomorphies that would indicate a close relationship of the seven families to the Cranchiidae, however, is not yet known. Young & Roper (1968) believed that a simple ridge-and-groove funnel locking apparatus is the primitive oegopsid condition, but they also thought that the other types of locking (or fusion) arrangements may have been derived independently. Furthermore, because a ventral attachment of the buccal connectives to arms IV also occurs in the myopsids as well as the majority of the oegopsids, this character likewise provides but weak justification for our choice of cranchiid outgroups. Nevertheless, some manageable basis for comparisons had to be established in order to implement our analyses, and the two characters cited above are among the few available on which to base such a selection.

Ontogenetic precedence: In the absence of unambiguous results from the outgroup comparisons, relative primitiveness is estimated on the basis of developmental data; the ontogenetically antecedent character state is hypothesized to be primitive while ontogenetically subsequent alternative expressions are hypothesized to be derived. In effect, we assume that evolutionary novelties are, more often than not, developmental modifications of phylogenetically ancestral conditions. Examples of neoteny and paed-

Character Number(s)	Tree
1	$\begin{array}{c} c \\ \uparrow \\ b < a > d \end{array}$
2, 3	$d < a > b > c$
4, 5, 7, 8, 12, 13	$a > b$
6	$b < a > c > d > e > f$
9, 11	$a > b > c$
10	$b < a > c$
14	$\begin{array}{c} c \quad d \\ \swarrow \quad \searrow \\ b < a > e > f \end{array}$

FIG. 1. Tree diagrams illustrating the estimates of polarity of states of characters described in the text. Hypotheses of polarity are presented in the right-hand column, and the characters whose states are believed to have evolved in the sequences illustrated are listed to the left.

genesis would provide obvious exceptions to this generalization; two cases of apparent paedomorphosis in cranchiid phylogeny are discussed below.

The (two or more) derived conditions of multistate characters were arranged, whenever possible, as geometrical or topological series (e.g., Character 6, Fig. 1) that could reasonably be expected to represent the sequential order of appearance of advanced states from the plesiomorph under a gradualistic model of phyletic change. Where no such series could be discerned (e.g., Characters 1 and 14, Fig. 1), all non-primitive states were regarded as independently derived by default. Multistate characters were then subjected to an additive binary recoding procedure (see Farris *et al.*, 1970) that reduces transformation series (morphoclines) with t states to $t-1$ binary (two-state) factors while preserving all of the phyletic information contained in the original character state tree topology. Table 1 presents the distribution of states of the origi-

nal, unfactored characters among the cranchiid genera, Fig. 1 provides diagrams of character state trees, and Table 2 is the data matrix that results from application of binary recoding to the character state distribution of Table 1 given the character state tree topologies of Fig. 1. Binary factors of multistate characters are labelled with the name of the character state that is the apomorph for the transformation represented by the factor. Thus, binary factor 6d of Table 2 represents the character state transition ($c \rightarrow d$) of Character 6; cranchiid genera with a score of (1) for binary factor 6d exhibit either state (d) of Character 6 or one of the two other states derived from (d) in the state tree for Character 6 (Fig. 1).

2. Inferring Tree Topologies

Numerous quantitative methods have been proposed to construct hierarchical arrangements of organisms, but only a few are directly pertinent to the problem of deriving well-corroborated hypotheses of phylogeny. Phenetic clustering algorithms, typically applied to matrices of overall similarity measures, do not address phylogenetic inference *per se* and are not employed here; Colless (1970) has argued that phenograms sometimes provide reasonable estimates of phylogeny, but the set of assumptions under which they may be presumed to do so seems to us unnecessarily onerous. Of explicitly phylogenetic methods we have chosen two that operationalize, at least in part, the analytic procedures of Hennig (1966).

The Wagner Tree method (Kluge & Farris, 1969; Farris, 1970) implements a heuristic procedure for discovering the most parsimonious hypothesis of phylogeny for a study collection of organisms and a set of cladistic characters. A most parsimonious phylogeny is defined to be that tree topology that requires the least number of convergent or reversed evolutionary events in order to derive the character state distributions observed among the extant organisms of the study from the hypothesized morphology of the common ancestor. Unlike earlier parsimony approaches (for example, Camin & Sokal, 1965), the Wagner method does not assume that evolution is irreversible, and for this reason we regard it as the more biologically reasonable. Caveats regarding uncritical use of the Wagner Tree method, however, have recently been offered by researchers (e.g.,

TABLE 1. Primary data matrix. Columns represent cranchiid genera; rows represent characters as numbered and described in the text. The entry for a given column \times row is the character state label appropriate to the corresponding genus and character. Abbreviations of taxa for this and the subsequent tables and figures: *Cra*, *Cranchia*; *Lio*, *Liocranchia*; *Lea*, *Leachia*; *Hel*, *Helicocranchia*; *Bat*, *Bathothauma*; *San*, *Sandalops*; *Lig*, *Liguriella*; *Tao*, *Taonius*; *Gal*, *Galiteuthis*; *Mes*, *Mesonychoteuthis*; *Ege*, *Egea*; *Meg*, *Megalocranchia*; *Teu*, *Teuthowenia*.

Character number	Taxa												
	<i>Cra</i>	<i>Lio</i>	<i>Lea</i>	<i>Hel</i>	<i>Bat</i>	<i>San</i>	<i>Lig</i>	<i>Tao</i>	<i>Gal</i>	<i>Mes</i>	<i>Ege</i>	<i>Meg</i>	<i>Teu</i>
1	d	d	d	c	c	c	a	a	a	a	b	b	a
2	a	b	a	a	d	a	b	c	c	c	c	c	c
3	a	a	a	d	d	a	a	b	b	b	c	c	c
4	b	b	b	a	a	a	a	a	a	a	a	a	a
5	a	a	b	b	b	b	b	b	b	b	a	a	b
6	b	b	b	c	c	d	d	e	e	e	e	e	f
7	a	a	a	b	b	b	b	b	b	b	b	b	b
8	b	b	b	a	a	a	a	a	a	a	b	b	b
9	a	a	a	a	a	a	a	b	c	c	a	a	a
10	a	a	a	a	b	b	b	a	a	a	a	c	a
11	c	c	a	c	c	c	c	b	b/c	c	b	a	b
12	b	b	b	a	a	a	a	a	a	a	a	a	a
13	a	a	b	b	b	b	b	b	b	b	b	b	b
14	b	b	d	e	f	a	e	e	e	e	c	c	e

Colless, 1980, but see also Mickevich & Farris, 1981) who report that applications of the algorithm to some data yield phylogenetic reconstructions that are not uniquely most parsimonious; other, equally or more parsimonious hypotheses of evolutionary relationships may exist, and consideration of plausible alternative methods of phylogenetic inference are therefore of interest.

The method of Character Compatibility Analysis (Estabrook *et al.*, 1977; Meacham, 1980) rests on the concept of the compatibility of cladistic characters (see also Estabrook, 1972). Two cladistic characters are said to be compatible if there exists at least one hypothesis of phylogeny for the organisms of the study collection that both can support. Thus, if two characters are incompatible, then both cannot support historical truth; at least one (and perhaps both) has undergone homoplasy in the course of the evolution of the study collection. All characters that support true statements of phylogenetic relationships, however, must be mutually compatible, while characters that do not support historical truth may or may not be pairwise compatible with each other and/or with true characters. Given a study collection of organisms and a set of cladistic characters, the compatibility of all character pairs can be analyzed and groups (cliques) of mutually compatible characters identified. For any clique of mutually compati-

ble characters there exists at least one phylogeny that all member characters can support, and that tree supported by the largest clique is sometimes chosen as the best estimate of true evolutionary history. In this study, Character Compatibility Analysis was used to develop alternative hypotheses of phylogeny to be tested against the results of Wagner analyses.

Minimum tree lengths and estimates of hypothetical ancestral phenotypes were calculated using the parsimony-optimizing procedure proposed by Farris (1970) subject to the constraint that the most recent common cranchiid ancestor exhibit the primitive morphology determined *a priori* by the methods of individual character analysis described above.

The computer programs we used to execute the Wagner analyses were written by J. S. Farris; the program for Character Compatibility Analysis was written by K. L. Fiala and G. F. Estabrook. Analyses were performed on the Michigan Terminal System at the University of Michigan.

RESULTS

1. Character Descriptions and Analyses

Character 1. *Funnel-mantle fusion cartilages*:

TABLE 2. Factored data matrix. Columns are labelled as in Table 1. For an explanation of factor labels and table entries, see the Methods section of the text.

Factor label	Taxa												
	<i>Cra</i>	<i>Lio</i>	<i>Lea</i>	<i>Hel</i>	<i>Bat</i>	<i>San</i>	<i>Lig</i>	<i>Tao</i>	<i>Gal</i>	<i>Mes</i>	<i>Ege</i>	<i>Meg</i>	<i>Teu</i>
1b	0	0	0	0	0	0	0	0	0	0	1	1	0
1c	0	0	0	1	1	1	0	0	0	0	0	0	0
1d	1	1	1	0	0	0	0	0	0	0	0	0	0
2b	0	1	0	0	0	0	1	1	1	1	1	1	1
2c	0	0	0	0	0	0	0	1	1	1	1	1	1
2d	0	0	0	0	1	0	0	0	0	0	0	0	0
3b	0	0	0	0	0	0	0	1	1	1	1	1	1
3c	0	0	0	0	0	0	0	0	0	0	1	1	1
3d	0	0	0	1	1	0	0	0	0	0	0	0	0
4b	1	1	1	0	0	0	0	0	0	0	0	0	0
5b	0	0	1	1	1	1	1	1	1	1	0	0	1
6b	1	1	1	0	0	0	0	0	0	0	0	0	0
6c	0	0	0	1	1	1	1	1	1	1	1	1	1
6d	0	0	0	0	0	1	1	1	1	1	1	1	1
6e	0	0	0	0	0	0	0	1	1	1	1	1	1
6f	0	0	0	0	0	0	0	0	0	0	0	0	1
7b	0	0	0	1	1	1	1	1	1	1	1	1	1
8b	1	1	1	0	0	0	0	0	0	0	1	1	1
9b	0	0	0	0	0	0	0	1	1	1	0	0	0
9c	0	0	0	0	0	0	0	0	1	1	0	0	0
10b	0	0	0	0	1	1	1	0	0	0	0	0	0
10c	0	0	0	0	0	0	0	0	0	0	0	1	0
11b	1	1	0	1	1	1	1	1	1	1	1	0	1
11c	1	1	0	1	1	1	1	0	0/1	1	0	0	0
12b	1	1	1	0	0	0	0	0	0	0	0	0	0
13b	0	0	1	1	1	1	1	1	1	1	1	1	1
14b	1	1	0	0	0	0	0	0	0	0	0	0	0
14c	0	0	0	0	0	0	0	0	0	0	1	1	0
14d	0	0	1	0	0	0	0	0	0	0	0	0	0
14e	0	0	0	1	1	0	1	1	1	1	0	0	1
14f	0	0	0	0	1	0	0	0	0	0	0	0	0

- (a) stout, roughly oval, subtriangular or spindle-shaped;
 (b) elongate, triangular;
 (c) narrow, straight;
 (d) fused into ventral cartilaginous strips.

In the Cranchiidae, the mantle is fused to the funnel at its posterolateral corners along two acutely diverging lines. These lines of fusion, found only in the cranchiids, replace the diverse forms of funnel-mantle locking cartilages present in all other teuthoids. In all members of the Cranchiinae, external cartilaginous strips, located on the ventral surface of the mantle, extend along one (the dorsal-most: *Leachia*) or both (*Cranchia*, *Liocranchia*) of the paired internal lines of funnel-mantle fusion and probably serve to strengthen the attachments (Fig. 2.4). The strips may run for partial or full length of, or beyond, the

lines of fusion. In *Cranchia*, these external strips are short, of coequal length and smooth except for a multipointed apical tubercle, while in *Liocranchia* they are relatively long, of coequal or unequal length, and tuberculate for their full extent. In *Leachia*, the strips are always tuberculate and vary, among the species of that genus, from about 10 to 50 per cent of the mantle length.

Outside of the cranchiids, fusion of the funnel and mantle occurs in only two other teuthoid genera: *Symplectoteuthis* (Ommastrephidae) and *Grimalditeuthis* of the monotypic family Grimalditeuthidae. In *Symplectoteuthis*, only the posterior portion of the funnel-mantle locking cartilages are fused, while in *Grimalditeuthis* there is complete fusion of the cartilages. In the Taoniinae, only remnants, termed funnel-mantle fusion cartilages, remain of the typical, separate locking

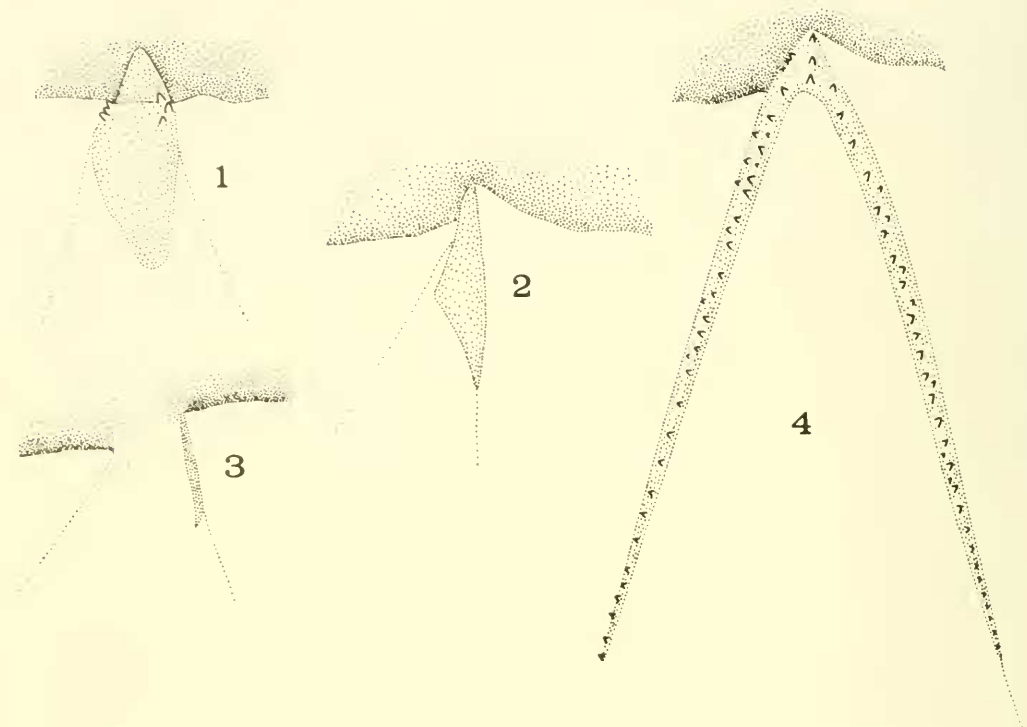


FIG. 2. Funnel-mantle fusion cartilage, left: (1) *Galiteuthis glacialis*, Elt 1112 (USNM), adult, 395 mm mantle length; (2) *Egea inermis*, WH 467-71 (ZMH), adult, 260 mm mantle length; (3) *Bathothauma lyromma*, AD 329-79 (ZMH), subadult, 190 mm mantle length; (4) *Liocranchia reinhardtii*, CI 71-98 (USNM), subadult, 160 mm mantle length. Dotted lines trace internal lines of funnel-mantle fusion; full extent of fusion lines not shown (see Character 1).

cartilages of non-cranchiid teuthoids. Funnel-mantle fusion cartilages cannot be identified as separate elements in the Cranchiinae, but it seems probable that such cartilages were the points of origin from which the ventral cartilaginous strips evolved.

The funnel-mantle fusion cartilages and the derived strips are the only known instances of cartilaginous elements present externally at the two funnel-mantle junctions. Among other teuthoids, with the exception of *Symplectoteuthis* and *Grimalditeuthis*, the locking apparatus consists of two separate, complementary, internal elements—one on the mantle and the other on the funnel. In the majority of oegopsid families, the locking apparatus is a simple, straight groove-and-ridge arrangement that was hypothesized to be primitive for the order by Young & Roper (1968). In two families, Ommastrephidae and Thysanoteuthidae, the locking apparatus is \perp - or \dashv -shaped; in the remaining six families, which

together with the Thysanoteuthidae comprise the outgroup, the funnel locking apparatus is round, oval, or subtriangular in shape.

The form of the funnel-mantle fusion cartilages varies within the Taoniinae. In *Helicocranchia* and *Bathothauma*, where the external funnel-mantle fusion area is markedly broad, the cartilage is straight, very slender and barely discernible (Fig. 2.3). In *Sandalops*, where the external fusion area is not broad but narrow as in the other taoniins, the cartilage is also straight, but distinct, and is shorter and wider than in *Helicocranchia* and *Bathothauma*. In all three genera, the cartilage (coded as "narrow, straight," above) follows the dorsalmost of the two internal lines of funnel-mantle fusion. The cartilage in *Egea* and *Megalocranchia* is elongate and triangular, with the longest side following the dorsalmost internal line of fusion (Fig. 2.2). In the remaining five taoniin genera, *Liguriella*, *Taonius*, *Galiteuthis*, *Mesonychoteuthis* and

Teuthowenia, the cartilage is stouter, varies considerably in shape, and is positioned more apically with respect to the internal lines of fusion, the long axis of the cartilage sometimes tending to follow the ventralmost line (Fig. 2.1). In this group of five genera, the cartilage also bears tubercles on the anterior end. These are present only in the young of *Mesonychoteuthis* and of some species of *Taonius*, but are present in both young and adults of *Liguriella*, *Teuthowenia* and most species of *Galiteuthis*. Because the more apical position and generally stouter outline of the fusion cartilage in these five genera most closely approaches the orientation and shape of the funnel-mantle locking cartilages among members of the outgroup, the character state to which we have assigned these squids is judged to be primitive for the extant cranchiids, and the remaining four states are hypothesized to have been independently derived.

Character 2. *Posterior end of gladius:*

- (a) conus present in larva and adult;
- (b) conus present in larva, lost or obscured in pseudoconus of adult;

- (c) conus lacking, pseudoconus present in larva and adult;
- (d) conus and pseudoconus absent.

Re-evaluation of the shape of the posterior end of the gladius of adults and a careful examination of the gladius in the larvae of all of the cranchiid genera have revealed anatomical differences in addition to those described earlier (N. Voss, 1980: Table 1). Voss described the character states: a) short conus; b) medium to long conus; and c) conus lacking, but did not distinguish between the two types of "conus" that occur within the family: 1) a "true" conus that exhibits no evidence of fusion or convergence of the edges of the gladiol vanes along the ventral midline, and 2) a pseudoconus formed by the infolding of the posterolateral margins of the gladiol vanes that converge along the midventral line, with or without subsequent fusion (Fig. 3). The definition of pseudoconus has been expanded here from that of McSweeney (1978) in order to include the instances of ontogenetically subsequent fusion that follow infolding in some cranchiids (N. Voss, 1980), and in some families of the outgroup and of other

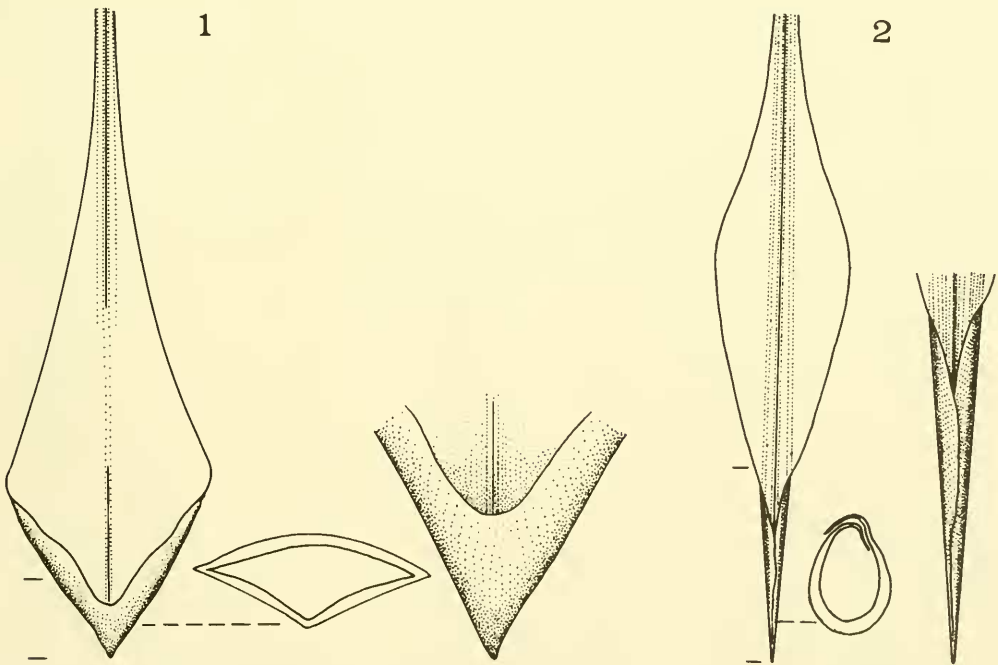


FIG. 3. Posterior end of gladius, ventral view, showing: (1) conus with enlarged cross-section and detail of *Sandalops* sp. B, WH 443-71 (ZMH), adult, 144 mm gladiol length; (2) pseudoconus with enlarged cross-section and detail of *Teuthowenia megalops*, B 6 (NBS), adult, 254 mm gladiol length (see Character 2).

oegopsids. In all observed cases, a fusion line is distinguishable. Among extant teuthoids, the conus portion of the gladius, presumably a vestige of the ancestral phragmacone, may be very small, or is sometimes found only in the young, or may be entirely absent (Naef, 1921/1923). All three conditions, in addition to the formation of a pseudoconus, are encountered among cranchiids.

Among members of the outgroup, a gladius with a narrow, usually elongate pseudoconus is typical of the Chiroteuthidae, Grimalditeuthidae, Mastigoteuthidae and Joubiniteuthidae. Specimens of three of the four nominal cycloteuthid species were examined; the gladius has what appears to be a true conus in one species, a pseudoconus in a second species and neither a conus nor a pseudoconus in a third species. In the little known Promachoteuthidae, a gladius with what appears to be a weakly-formed conus is found in an unnamed species (R. Toll, personal communication). Thysanoteuthids have a weakly formed conus in the young stages (R. Toll, personal communication) but lack both conus and pseudoconus in the adults. A pseudoconus is also found in three other oegopsid

families that do not belong to the outgroup: Lepidoteuthidae, Brachiotheuthidae and Batotheuthidae.

Even though a pseudoconus is the commoner structure in the outgroup, we believe that the presence, in larva and adult, of a small conus displaying no evidence of mid-ventral fusion or convergence of the lateral margins of the vanes is primitive for cranchiids. We would support this judgment by the observation that, where both conus and pseudoconus are sequentially exhibited in the ontogeny of extant cranchiids, it is the conus that is invariably precedent and the pseudoconus that is developmentally subsequent. The absence of both conus and pseudoconus, a condition found only in *Bathothauma*, we judge to have been derived independently from the primitive state. This judgment is based on the unique modification of the posterior end of the gladius in *Bathothauma* in which the vanes are transformed into a transverse bar that gradually expands laterally to shovel-shaped ends on which the fins insert (Fig. 4.4). An elongation of the posterior end of the conus in *Leachia* and *Helicocranchia* serves to extend support for the

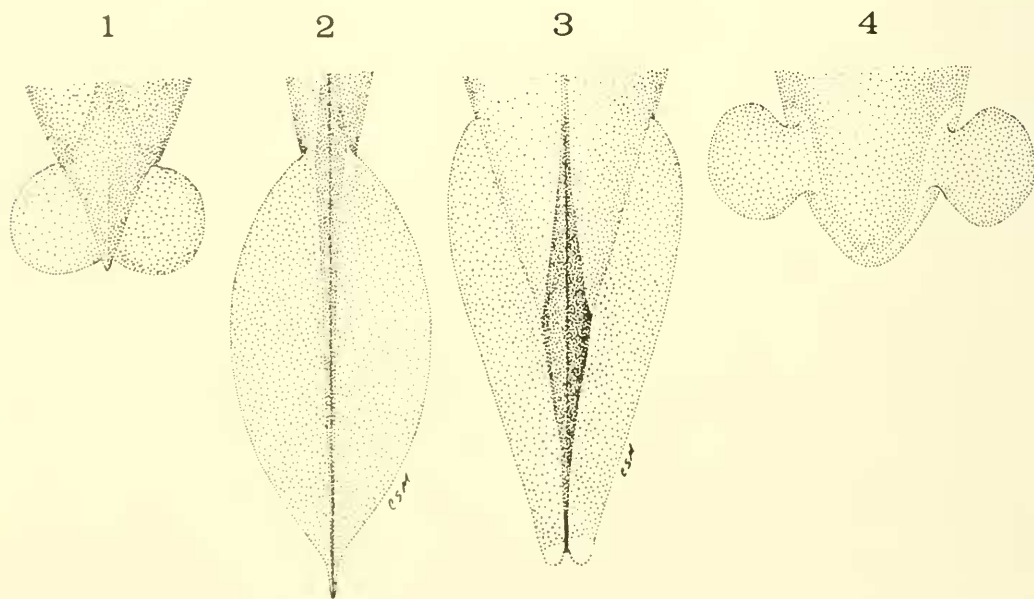


FIG. 4. Posterior end of mantle, dorsal view, showing variation in shape of fins: (1) *Sandalops* sp. C, CI 71-6-26 (USNM), adult, 102 mm mantle length; (2) *Galiteuthis glacialis*, Elt 1323 (USNM), adult, 333 mm mantle length; (3) *Teuthowenia megalops*, B 17 (NBS), adult, 352 mm mantle length; (4) *Bathothauma lyromma*, O 4713 (UMML), subadult, 165 mm mantle length (1-3 from N. Voss, 1980) (see Character 3).

fins; it is a solid structure and does not appear to be homologous with the hollow pseudoconus.

Character 3. *Shape of fins*:

- (a) elliptical, oval or circular, terminal;
- (b) lanceolate or stout, ovate, terminal;
- (c) lanceolate or long-narrow, terminal-lateral;
- (d) small, paddle-shaped, subterminal.

Ontogenetically, the fins develop from the shell fold (Naef, 1921/1923). In the early larva of all cranchiids, the fins are small, separate and paddle-shaped. They then typically become longer and rounded with growth, later become contiguous, and finally elongate to varying degrees to accompany the elongation of the posterior end of the gladius.

While growth of the oegopsid fin is typically anterior, fin growth among cranchiids is typically posterior. The fins are terminal, elliptical, oval or circular in all genera in which the conus is present in the larvae (Fig. 4.1), with the exception of *Helicocranchia*. With ontogenetic disappearance of the conus, the fins are extended posteriorly on the developing pseudoconus and assume a generally lanceolate form. They remain terminal in *Taonius*, *Galiteuthis* and *Mesonychoteuthis* (Fig. 4.2), while in *Egea*, *Megalocranchia* and *Teuthowenia*, they simultaneously grow anteriorly on the mantle to become terminal-lateral (Fig. 4.3). The musculature of the fins is usually poorly developed except in *Mesonychoteuthis* in which the fins become stout and ovate in shape, and very muscular medially.

The form of the fins in the outgroup varies considerably. The typical shape is elliptical, oval or circular, with the marked exception of thysanoteuthids in which the fins are rhomboid. The fins may be subterminal, terminal, terminal-lateral or extended to nearly the full length of the body. The pseudoconus often projects beyond the posterior margins of the fins as a slender to needle-like tail of varying length; this structure may bear a supplementary, or auxiliary finlike structure.

On the basis of its ontogenetic precedence, the state of "elliptical, oval or circular, terminal" fins is considered to be primitive for extant adult cranchiids. The common developmental trend in the family toward posterior elongation of the fins with support afforded by a lengthening pseudoconus, together with the subsequent occurrence (in three genera) of anterior growth to form terminal-lateral fins, is

interpreted to reflect the evolutionary sequence of appearance of these conditions in cranchiid phylogeny. The retention, into adulthood, of the larval state of small, paddle-shaped fins in *Helicocranchia* and *Batho-thauma* (Fig. 4.4) is interpreted to represent a neotenuous condition independently derived from the primitive state.

Character 4. *Funnel-head fusion*:

- (a) funnel not fused to head laterally;
- (b) funnel fused to head laterally.

In the Cranchiidae, lateral fusion of the funnel to the head occurs only in *Cranchia*, *Liocranchia* and *Leachia*. The funnel is free laterally in all members of the Taoniinae. Among other teuthoids, additional instances of the fused state are found in the Bathyteuthidae and in the sole member of the Joubiniteuthidae; the Ommastrephidae, and some members of the Chiroteuthidae and Mastigoteuthidae also display varying degrees of lateral fusion. In the majority of teuthoids, however, including members of the remaining four outgroup families, the funnel is free laterally. The free, unfused condition is tentatively interpreted as primitive for the family Cranchiidae, and the fused condition as derived.

Though the functional significance of the varying degrees of lateral fusion is not known, it presumably relates to the role that the funnel plays in locomotion in the different groups.

Character 5. *Funnel valve*:

- (a) present;
- (b) absent.

A valve with a free anterior margin is found on the inner, dorsal surface of the anterior part of the funnel in all Cephalopoda except for the Octopoda and some genera of the Teuthoidea: *Valbyteuthis* (Chiroteuthidae) and nine of the thirteen cranchiid genera. Among cranchiids, a funnel valve is found only in *Cranchia*, *Liocranchia*, *Egea* and *Megalocranchia*. Considering its near universal occurrence among all other oegopsids, it is inferred that a funnel valve was likely found in the most recent common ancestor of the extant cranchiids and, therefore, would best be considered primitive for the family.

Though it is commonly believed (Naef, 1921/1923) that the valve functions to prevent water from entering the funnel when the mantle is being expanded, Zuev (1967) as-

sociated the absence of a valve with the loss of the ability to swim headfirst (forward movement).

Character 6. *Ocular photophores*:

- (a) unknown, extinct;
- (b) four or more, small, simple photophores;
- (c) one, large, complex photophore;
- (d) one large plus one small, contiguous, complex photophore;
- (e) one large plus one small, non-contiguous, complex photophore;
- (f) one large plus two small, non-contiguous complex photophores.

Ocular photophores, found also in many other families of teuthoids, occur in all members of the Cranchiidae (Fig. 5). Three changes have here been made in the character state coding employed by N. Voss (1980: Table 1). Firstly, newly-acquired taoniin specimens show that the first small, non-contiguous photophore grades from "short" to "long-narrow," without the distinct break that was formerly thought to occur in the group. As a result, the states originally described as "one large plus one small, short non-contiguous photophore" and "one large plus one long, narrow non-contiguous photophore" have been united to read "one large plus one small, non-contiguous, complex photophore." Secondly, an additional new state "one large plus two small, non-contiguous, complex photophores" is coded for the unique condition exhibited by *Teuthowenia* (described in a footnote in the original table). Thirdly, more detailed study of photophore morphology has resulted in the insertion of "simple" and "complex" to express important differences subsequently observed.

Between the Cranchiinae and the Taoniinae, there are differences in the appearance, structural morphology, photogenic material and ontogeny of the ocular photophores. In the Cranchiinae, the organs are small, round to oval in shape, and relatively simple in structure (Fig. 5.5), comprised of apparently ectodermal invaginations that retain their connections with the ectodermal epithelium (Chun, 1910); consequently, the cup of photogenic tissue has direct contact to the exterior. By contrast, taoniin photophores are markedly dissimilar in size, one of them is usually crescent- or sickle-shaped, and all are more complex in structure than the corresponding organs among cranchiins. The photogenic tis-

sue in taoniins is embedded below the surface of the photophore in a narrow band along one margin, with the emitted light spread over the wide surface of the organ by means of a thick layer of light guides (Dilly & Herring, 1974; Dilly & Nixon, 1976; Herring, 1977). Studying the ocular photophore in *Bathothauma*, Dilly & Herring (1974) found that the photogenic tissue contained paracrystalline material. Herring (1977) later reported the same material in the ocular organs of *Egea* and *Megalocranchia* (correct generic identifications for Herring's *Phasmatopsis lucifer* and *P. oceanica* respectively) and considered that it probably occurs in all taoniins, in contrast to the cranchiins in which it does not occur.

Larvae of the majority of cranchiid species, including representatives of every genus, were examined. In all members of the Cranchiinae, the ocular photophores first appear as separate organs in their approximate final adult position. They make their appearance in the developing young in groups or singly over varying periods of time until the definitive adult pattern is attained. This is not the case in the Taoniinae. In all of the taoniins, a single, poorly-defined patch first appears on the narrow, posteroventral end of the oval, stalked eye of the larva. With growth, the photophore becomes better defined and enlarges to conform approximately to the ventral surface of the eye. This is the only photophore that develops in *Helicocranchia* and *Bathothauma* (Fig. 5.1), but in the other genera (Fig. 5.2-5.3) a second and, in *Teuthowenia* (Fig. 5.4), a third small organ forms as the eye enlarges and gradually becomes sessile and near-hemispherical in shape. In the larvae of *Taonius*, *Galiteuthis*, *Mesonychoteuthis* and *Teuthowenia* (Fig. 5.6-5.9), the initial photophore patch extends from the undersurface to along the edge of the narrow, posteroventral end of the eye. Along this edge a thickening and a break occur in the patch to form the second organ which then gradually separates and assumes the final position. The third organ in *Teuthowenia* splits off from the inner end of the second organ as it, in turn, separates from the first.

In *Sandalops*, *Liguriella*, *Egea* and *Megalocranchia*, the narrow, posteroventral end of the oval larval eye is extended by a pronounced cone-shaped rostrum, or ocular appendage, that J. Young (1970) found (in *Bathothauma*) to be filled with loose connec-

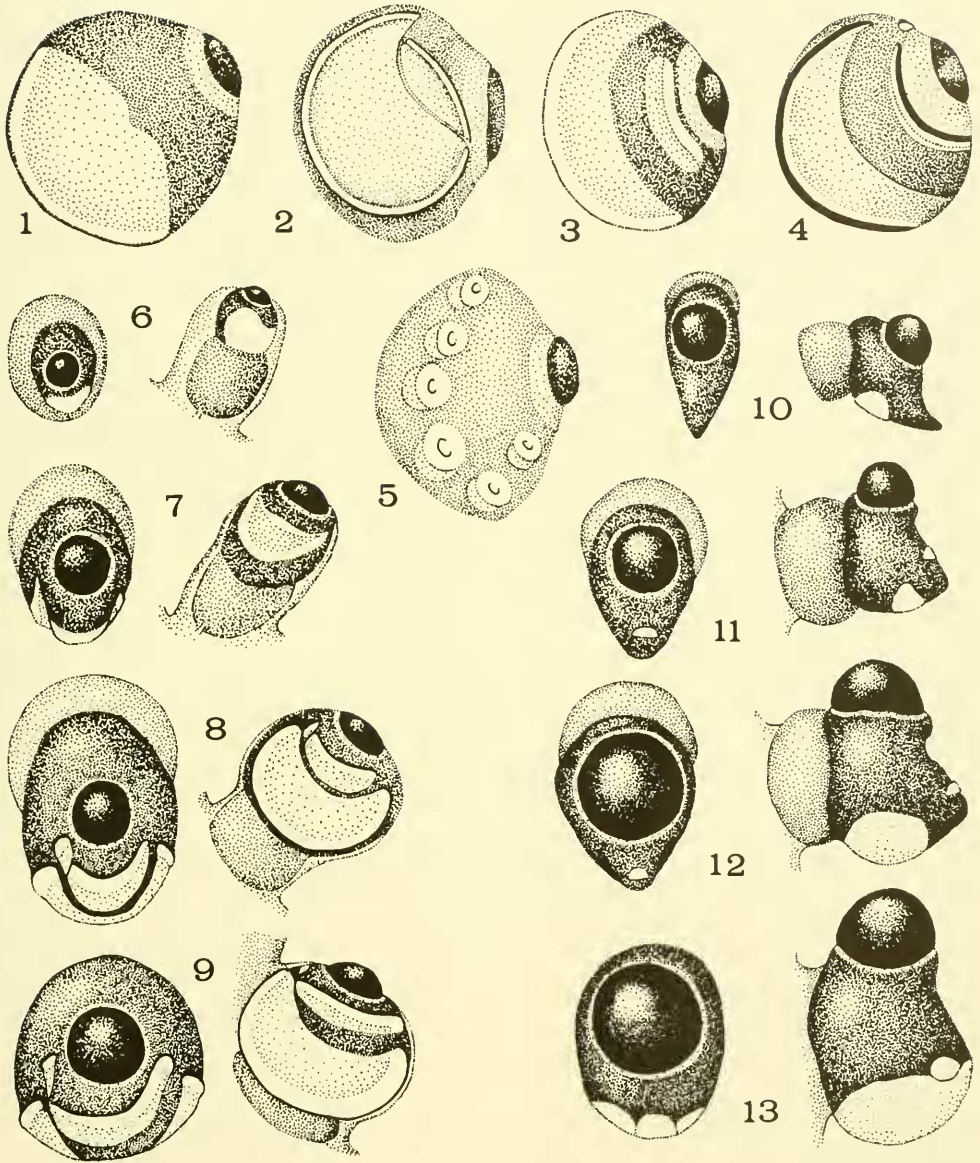


FIG. 5. Eye, left, showing variation in shape of ocular photophores: (1) *Bathothauma lyromma*, O 4713 (UMML), subadult, 165 mm mantle length; (2) *Liguriella podophtalma*, WH 417-1-71 (ZMH), subadult, 243 mm mantle length; (3) *Galiteuthis glacialis*, Eit 1323 (USNM), adult, 333 mm mantle length; (4) *Teuthowenia* sp. B, WH 417-71 (ZMH), subadult, 154 mm mantle length; (5) *Leachia atlantica*, IOM 1880, adult, 105 mm mantle length. (6-9) *Teuthowenia* sp. B, ontogenetic series showing development of ocular photophores, anterolateral and ventral views of left eye: (6) Eit 1776 (USNM), 7 mm mantle length; (7) Eit 2270 (USNM), 27 mm mantle length; (8) DMNZ, 60 mm mantle length; (9) SAM A31421, 81 mm mantle length. (10-13) *Sandalops* sp. C, ontogenetic series showing development of ocular photophores, anterior and ventrolateral views of left eye: (10) F II (USNM), 27 mm mantle length; (11) Eit 31-24A (USNM), 26 mm mantle length; (12) F IV (USNM), 33 mm mantle length; (13) F IV (USNM), 38 mm mantle length (2 from Voss, 1980) (see Character 6).

tive tissue. R. Young (1975b) described a somewhat different development of the photophores in *Sandalops* (Fig. 5.10–5.13). The first, large organ appeared as a patch on the underside of the rostrum, but did not extend to the edge of the apex. With growth, the rostrum progressively shortened until only a remnant remained, on top of which a second ocular photophore appeared. With the disappearance of the rostrum, the second organ assumed a contiguous position with the first. An examination of the larvae of *Liguriella*, *Egea* and *Megalocranchia* demonstrated a similar type of development, but in the latter two genera, the second organ subsequently separates from the first as the eye becomes sessile, while in *Liguriella* and *Sandalops* the two photophores remain contiguous. N. Voss (1974) did not have an adequate series of larvae with intact eyes to show the details of development of the ocular photophores in *Egea*. It appears that the separate development of the two photophores in the above four taoniin genera is a result of the penetration and subsequent division of the tissue of the photophore patch at an early stage by the development of a pronounced ocular rostrum.

The majority of the ocular photophores found among the other teuthoids are of the complex type, with the surface layer of light guides diffusing the light from a photogenic core, similar to that found in the taoniins (Herring, 1977). This is supported by our investigations. In the outgroup, ocular photophores are found in the Chiroteuthidae (majority of species), Mastigoteuthidae (one out of numerous species) and the Cycloteuthidae (two out of four nominal species). They are not found in the Promachoteuthidae. In Grimalditeuthidae, Joubiniteuthidae, the juvenile state of Thysanoteuthidae and a few members of the Chiroteuthidae, there is a broad, usually thick, highly reflective, gold band surrounding the lens and often extending around the ventral surface of the eye. Whether this band contains luminous tissue in any of the groups was not determined. In the Chiroteuthidae, ocular photophores may occur as long bands, small round organs arranged in rows, or bands of what appear to be incompletely separated round organs. The situation suggested to Herring (1977) that the separate round organs coalesce to form the long bands. Instead, the opposite may occur as in the taoniins, where several small organs are derived, at least ontogenetically, from a single large one. Naef (1921/1923) suggested that

the primitive form for ocular photophores in cephalopods "may be a diffuse luminescence of the whole skin of the eyeball."

The marked differences in the structure and ontogeny of the ocular photophores between the cranchiids and the taoniins suggest separate lines of development. A common ancestral state cannot be confidently identified from among the conditions exhibited by extant cranchiids, and is therefore presumed to be extinct. The ontogenetic findings reported here suggest the existence of a single evolutionary trend towards photophore fragmentation in the Taoniinae; the character state "one large, complex photophore" is therefore judged to be the most primitive for this morphocline.

The ocular photophores of cranchiids appear to function, at least in part, as a ventral camouflage mechanism of advantage to the animal in avoiding predators (R. Young, 1975b).

Character 7. *Hectocotylus*:

- (a) present;
- (b) absent.

One or more arms of the males of many cephalopods are modified for courtship and copulation. The modification, commonly termed hectocotylyzation, may be symmetrical, equally affecting both arms of a pair, or asymmetrical, affecting only one arm or a pair of arms unequally. There is great diversity in the modification. It may involve the whole arm or only part of the arm and affect any or all of its features—suckers, sucker pedestals, protective membranes, general surface and overall shape and size.

The word "hectocotylus" was originally used for the autotomous third (right or left) arm found in certain families of pelagic incirrate octopods—Tremoctopodidae, Ocythoidae, Argonautidae and Alloposidae. The arm is used for insemination. During mating it detaches from the male and remains within the mantle cavity of the female, carrying with it the spermatophore of the male. In most other incirrate octopods, a lesser modification for insemination is found in which the terminal portion of the same third (right or left) arm is transformed into a discrete organ, called a ligula, which remains attached. This organ is not found in cirrate octopods (G. Voss, personal communication). Steenstrup (1857) considered that the autotomous structure found in *Tremoctopus* and the other pelagic

incirrate octopods mentioned above is but an elaborate modification of the sessile structure found in most of the remaining incirrates. This is supported by the ontogeny of the structure in *Tremoctopus* described by Thomas (1977). Instances of lesser symmetrical modification, such as enlarged suckers, are scattered throughout the octopods.

The Sepioidea and Teuthoidea display a wider diversity of both asymmetrical and symmetrical modifications of the male arms. The arms most strongly affected in these two groups are the first and fourth pairs, and, when the modification is asymmetrical, it always involves one of these pairs. In the Sepioidea, the modification is primarily asymmetrical and is found in most of the member families. In the Teuthoidea, asymmetrical modification occurs in both families of myopsids but is only known to occur in six of the twenty-three families of oegopsids—Enoploteuthidae, Lycoteuthidae, Architeuthidae, Ommastrephidae, Thysanoteuthidae and Cranchiidae. Various types of symmetrical modification of one or more arm pairs frequently occurs. The nature of the symmetrical modifications suggests a holding and caressing function. The asymmetrical modification occurs earlier in the ontogeny of the animal than do the symmetrical modifications which occur at varying later periods, some appearing just prior to maturity.

The word "hectocotylus" is commonly used for the single asymmetrical modified arm in the sepioids and teuthoids, which is known in some (and presumed in the remainder) to be used to transfer the spermatophores to the female either by directly grasping the spermatophores or by acting as a bridge. Robson (1926) doubted that the modified arm was used in the same way in the octopods as it is in the sepioids and teuthoids, and suggested that the so-called hectocotylus of the latter two orders be termed the nuptial arm. In the sepioids and teuthoids, there is no structure formed that may be termed an "organ" that is common to all members similar to that found in the octopods. Indeed, in some groups many of the details of the asymmetrical modified arm are so bizarre that it is difficult to imagine their function in handling spermatophores, and some appear to have developed for holding or tactile purposes, perhaps giving the arm a dual purpose. This is not inconsistent with the observed use of the modified arm in *Octopus* (Robson, 1926). In sepioids and teuthoids it is difficult to observe the exact use

of the arm because copulation occurs so rapidly. Spermatophores, however, have been observed on the modified arm during courtship in *Sepioteuthis* (Arnold, 1965), and transferred to the female by the modified arm during copulation in several species of *Loligo* (Drew, 1911; McGowan, 1954; Hamabe & Shimizu, 1957; Arnold, 1962). Thus it appears that the primary function of the asymmetrical modified arm of the male in these two orders is similar to that in octopods and therefore can be correctly called the hectocotylus, and asymmetrical modification of both arms of a pair can be referred to as hectocotylization. The occurrence and diversity of structure of the hectocotylus in the sepioids and teuthoids suggests that it is polyphyletically derived (Naef, 1921/1923). N. Voss (1980) called the symmetrical modification of arm pairs or all of the arms of the male "secondary sexual modification" to distinguish their known or presumed use of holding or caressing from the primary use of the hectocotylus.

The occurrence, position and general form of the hectocotylus are generally correlated with taxon membership (Steenstrup, 1857), and are usually constant within families. In the females of a number of groups, there are different structures for the reception of the spermatophores, sperm reservoirs or sperm that correspond to the particular arrangement of the hectocotylus and method of transfer of the spermatophores (Hoyle, 1907). On the grounds of its usually constant occurrence within a family, we have judged the presence of a hectocotylus to be primitive, and its absence to be derived in the Cranchiidae. In the cranchiids, a hectocotylus is only found in the three genera of the Cranchiinae (N. Voss, 1980; Figs. 1b, 2c, 3b). It occurs on the fourth (right or left) arm and is similar in appearance in all species. There is no special structure in the females of either subfamily for the reception of the spermatophores. Throughout the family, spermatophores appear to be transferred directly to the exterior dorsal surface of the mantle; sperm reservoirs have been found embedded in the mantle walls (occasionally in head and arms) and in various stages of emergence into the mantle cavity of mature females in *Liocranchia*, *Leachia*, *Helicocranchia*, *Bathothauma*, *Sandalops*, *Galiteuthis*, *Megalocranchia* and *Teuthowenia* (N. Voss, unpublished notes).

The symmetrical or secondary modifications of the arms of the males, which are compared in Table 2 of N. Voss (1980), are too

variable for use in this study. The modifications, however, are usually similar within a genus. They are more numerous in occurrence and variable in form in the Taoniinae than in the Cranchiinae.

Character 8. *Brachial end-organs*:

- (a) absent;
- (b) present.

The brachial end-organ is a leaf or spoon-shaped organ found on the distal ends of arm pairs in near-mature and mature females of some cranchiid genera (N. Voss, 1980; Fig. 3e). It occurs in all species of the Cranchiinae, and in all species of the taoniin genera *Egea*, *Megalocranchia* and *Teuthowenia*. Typically the end-organ appears when the female squid nears maturity and has descended into the deeper waters; at that time, the trabeculate protective membrane on both sides of the affected arms expands and becomes darkly pigmented. This process is accompanied by a reduction and eventual loss of the suckers, and the oral surface of the affected portion usually becomes rugose or spongy; the pedestals of the affected suckers may be lost or greatly modified. The end-organ varies in proportional size and extent of occurrence on the arms in the different species. Among the cranchiids, the organ occurs only on arms III in *Liocranchia* and in all of the species of *Leachia*, except for *L. danae*, and occurs on all of the arms in *L. danae* and in *Cranchia*; among the taoniids, it appears on arms III in *Egea* and in some species of *Megalocranchia* (rarely on arms II), on arms I, II and III in the remaining species of *Megalocranchia*, and on all of the arms in *Teuthowenia*. The organ ranges in size from about 5 to 30% of the arm length, and is approximately the same size on the different arms in a species, except in *Cranchia* where it is markedly disproportionately developed. It tends to be proportionally larger in the cranchiids than in the taoniids.

The brachial end-organ is reported to occur only in the Cranchiidae; the collections of the U.S. National Museum, however, contain two large teuthoids, a male and a female as yet unidentified to family, which both display long, similar-appearing organs on the ends of arms IV. In these specimens (kindly shown us by C. F. E. Roper), only the dorsal protective membrane of the arm is modified to form the organ, not the entire oral surface as among cranchiids. The mature stage is not known for many members of the outgroup, and it is possible that some will eventually be found to

have brachial end-organs. At this time, however, the presence of these peculiar structures seems best regarded as a derived condition for extant cranchiids since its absence is conspicuously more widespread among other teuthoids.

The brachial end-organ appears to be a photophore of unique structure that probably functions as a sexual attractant (R. Young, 1975a).

Character 9. *Clubs*:

- (a) without hooks;
- (b) with hooklike teeth on large suckers;
- (c) with hooks.

Hooks are found on the tentacular clubs in only four of the twenty-five families of teuthoids—the Cranchiidae, and three other families that are not presently thought to share recent common ancestry with cranchiids, Gonatidae, Enoploteuthidae and Onychoteuthidae. Hooks are not present on the clubs in any of the members of the outgroup. Among gonatids, hooks occur on the clubs in only one of the two genera where the adult morphologies of the clubs are known. In the large family Enoploteuthidae, hooks are found on the clubs of all species except for those of the genus *Pterygioteuthis*. In all onychoteuthid species, the clubs, where known, bear hooks. Of the thirteen genera belonging to the Cranchiidae, only two, *Galiteuthis* and *Mesonychoteuthis*, have hook-bearing clubs.

In all of the families in which they occur, the hooks are absent in the larvae and first appear in the early or midjuvenile stages. They are formed from typical suckers (Fig. 6.1) of the median one or two rows on the manus, and their appearance is often accompanied by a reduction or loss of the suckers of the marginal rows. The hooks develop by gradual enlargement of a median tooth on the distal margin of the sucker ring (Figs. 6.3–6.8). As the median tooth enlarges, incorporating the lateral teeth, the ring aperture is greatly reduced; in the process, the outer margin of the sucker is transformed into a hood for the hook. Among cranchiids, an intermediate stage between sucker and hook is found in the members of the genus *Taonius* (Fig. 6.2); in the postlarval animal, the suckers of the two median rows of the manus elongate and become greatly enlarged, with the distal margin of the sucker ring drawn out into one or two large, central, hooklike teeth. The aperture of the ring, however, is not reduced, and the

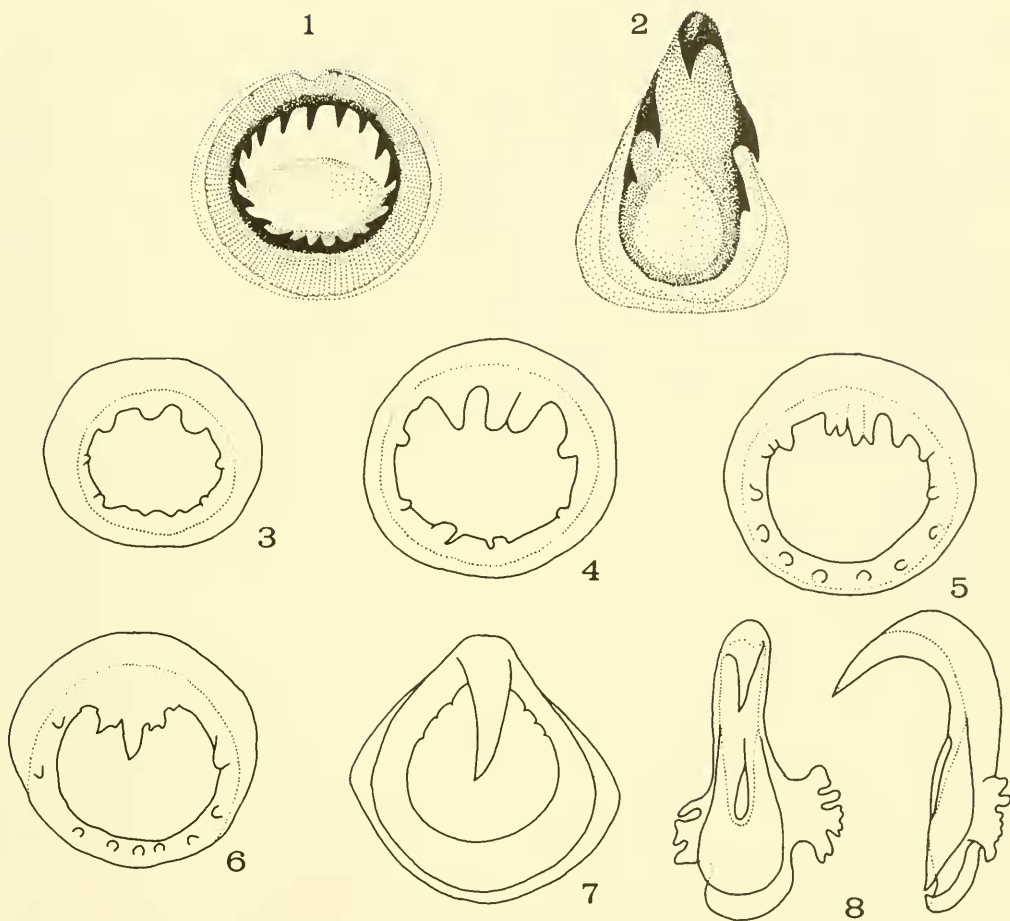


FIG. 6. Largest sucker from tentacular club of: (1) *Teuthowenia megalops*, WH 712-73 (ZMH), subadult, 187 mm mantle length; (2) *Taonius pavo*, O 4812 (UMML), adult, 540 mm mantle length. (3-8) *Galiteuthis glacialis*, ontogenetic series showing modification of ring from largest tentacular sucker to form hook: (3) Elt 697 (USNM), 29 mm mantle length; (4) SC 24-62 (USNM), 38 mm mantle length; (5) Elt 935 (USNM), 55 mm mantle length; (6) Elt 949, (USNM), 58 mm mantle length; (7) Elt 943 (USNM), 73 mm mantle length; (8) Elt H371 (USNM), 297 mm mantle length (3-8 redrawn from McSweeney, 1978) (see Character 9).

structure presumably can still function as a sucker in these species.

As the morphological sequence from sucker, to hooklike sucker, to hook appears to reflect increasing functional specialization, so also do the clubs on which the different structures are found; there is a progressive definition of a carpal sucker cluster, reduction of the suckers of the marginal rows of the manus, and reduction of the dactylus and the dorsal keel; the end result of this transformation series is a simpler and more efficient club for capturing and holding soft-bodied animals (Naef, 1921/1923). Ontogenetic evidence and out-group comparisons combine to sug-

gest that the ancestral state for the cranchiids is the club without hooks (i.e., solely with typical suckers); clubs with hooklike teeth on the suckers, as in *Taonius*, and clubs with well developed hooks, as in *Galiteuthis* and *Mesonychoteuthis*, appear to be successively derived conditions.

Character 10. *Digestive gland*:

- (a) stout, spindle-shaped;
- (b) elongate, spindle-shaped;
- (c) rounded, with a large photophore.

The digestive gland in oegopsids is usually stout and spindle- or ovoid-shaped, and lies at

an acute angle to, or parallel with, the longitudinal axis of the body. In the Cranchiidae, the digestive gland is spindle-shaped in all genera with the exception of the later growth stages of *Megalocranchia* species, and is suspended at a right angle to the longitudinal body axis. From dissections and from the literature it appears that this unusual position of the digestive gland, while common in oegopsid larvae, is found in the adults of only two other teuthoid families, both members of the outgroup—the Grimalditeuthidae, and in some species of the Chiroteuthidae. The elongation of the spindle shape of the gland, as found in the young and subadult of *Liguriella* (adult unknown) and in all growth stages of *Bathothauma* and *Sandalops*, appears derived from the stout, spindle shape that we hypothesize to be the primitive state for the cranchiids.

A large, rounded digestive gland with an associated compound photophore overlying the ink sac characterizes all members of the genus *Megalocranchia*. In the larva of *Megalocranchia*, the gland is typically stout and spindle-shaped, with the photophore first appearing in the late larva. With growth, the gland gradually becomes rounded and the photophore proportionally enlarges to cover the entire ventral surface. In the outgroup, a photophore is also found on the ink sac in a number of species of the Chiroteuthidae and in two of the four nominal species of the Cycloteuthidae. Nevertheless, the ontogenetic derivation of the condition found in *Megalocranchia* from the commoner photophore-less condition of the digestive gland seen among all other cranchiids would appear to argue that the presence of a photophore on the gland is an independently derived condition.

R. Young (1975b, 1977) suggests that the spindle shape and vertical orientation of the opaque digestive gland, by reducing the ventral countershading problem of the animal, and the photophore on the large, rounded digestive gland in *Megalocranchia*, by its countershading luminescence, are devices for ventral camouflage.

Character 11. *Digestive duct appendages:*

- (a) on ducts;
- (b) on ducts and digestive gland;
- (c) on digestive gland.

From the researches of Bidder (1966, 1976) and Schipp & von Boletzky (1975,

1976), among others, it appears that the structure and function of the digestive duct appendages, which are formed from the digestive ducts, differ between the Octopoda, Sepioidea and Teuthoidea, and can be related to the different position of the organ in each group. In octopods, the appendages are found on the posteroventral surface of the digestive gland and lie within its connective tissue envelope, while in the sepoids and teuthoids, the appendages are found outside of the envelope of the digestive gland and are covered by renal epithelium. Among sepoids, the digestive duct appendages always occur as grapelike follicles on the digestive ducts and are in close topical relationship with "renal" epithelium; by contrast, the position and gross morphology of the appendages are variable in the teuthoids, often within families and sometimes within genera. Greater variation is found among cranchiids than among members of the outgroup.

In the Cranchiidae, digestive duct appendages may occur on the ducts, on the ducts and digestive gland, or on the digestive gland alone. The state "on the ducts" is a correction of the state mistakenly described in Table 1 of N. Voss (1980) as "on posterior end of ducts or on caecum." The generic definitions given in the text and a re-examination of the specimens support this correction. The appendages appear in the form of two large, compound lobes on the posterior portion of the united duct in *Leachia*, and in the form of small clusters of follicles on the posterior portion of the separate ducts in *Megalocranchia*. In *Taonius*, *Egea*, *Teuthowenia* and two species of *Galiteuthis* the appendages are in the form of two large, compound lobes on the posterodorsal surface of the digestive gland at the exit of the digestive ducts and in the form of small clusters of follicles on the entire length of the ducts. In the remaining seven genera, *Cranchia*, *Liocranchia*, *Helicocranchia*, *Bathothauma*, *Sandalops*, *Liguriella*, *Mesonychoteuthis* and four species of *Galiteuthis*, the appendages occur as two large, compound lobes in the same position on the digestive gland as in the preceding group.

In the outgroup, the appendages appear as small clusters of follicles on the entire length of the ducts in Thysanoteuthidae, Cycloteuthidae (one species), Mastigoteuthidae (two species), Promachoteuthidae and Joubiniteuthidae. They appear as a thick coating of spongy tissue on the major or entire length of

the ducts in Chiroteuthidae (one species), Grimalditeuthidae and Cycloteuthidae (one species). In the remaining five species of chiroteuthids and five species of mastigoteuthids examined, the appendages occur as medium to large, compound lobes on portions of the ducts. Thus, it would appear that the position of the digestive duct appendages on the ducts is most parsimoniously regarded as ancestral for extant cranchiids, and that the presence of these appendages on the digestive gland is likely a derived condition.

The investigations of Schipp & von Boletzky (1975, 1976) suggest that the digestive duct appendages in the sepoids play a role in excretion and nutrient absorption as well as osmoregulation and urine formation. Our present lack of knowledge of the fine structure of the appendages in the teuthoids, however, precludes meaningful speculation on the functional significance of the differences in their position and gross morphology.

Character 12. *Caecum*:

- (a) smaller than stomach;
- (b) larger than stomach.

The relative size of the caecum and the stomach varies within the oegopsids. In the Cranchiidae, the caecum is larger than the stomach in the three genera of the Cranchiinae and is smaller than the stomach in the ten genera of the Taoniinae. An examination of as many members as possible of the outgroup revealed that the caecum is larger than the stomach in the Cycloteuthidae and the Promachoteuthidae, larger than or approximately the same size as the stomach in the Mastigoteuthidae, and is smaller than the stomach in the Thysanoteuthidae, Chiroteuthidae, Grimalditeuthidae and Joubiniteuthidae. Considering that the caecum is smaller than the stomach in the majority of the outgroup members, we are inclined to regard that state as primitive for the extant cranchiids.

The functional significance of the relative size differences of the caecum and the stomach is not known but might reflect differences in feeding habits (see Bidder, 1966).

Character 13. *Eyes of larvae*:

- (a) sessile;
- (b) stalked.

Stalked eyes are found in the larvae of all cranchiids with the exception of *Cranchia* and

Liocranchia. The length of the larval eye stalks and the period of their persistence varies considerably among the ontogenies of the different genera. Though markedly protruding eyes are found in the larvae of some teuthoids, for example, in the Octopodoteuthidae, Thysanoteuthidae and at least one of the four nominal species of Cycloteuthidae, there is no known occurrence of stalked eyes in cephalopod larvae outside of the Cranchiidae. The absence of stalked eyes in the larvae of all other known cephalopods (and of two genera of the Cranchiidae, and the variability of the character within the remaining members of the family) would indicate that sessile eyes may be considered primitive for cranchiids. N. Voss (1980), however, referred to the loss of the character of stalked eyes in *Cranchia* and *Liocranchia*. The present, broader analysis of this character, suggests that the contrary is true, i.e. that sessile eyes are retained in these two genera as an unmodified ancestral state and that the presence of stalked eyes in the remaining cranchiid genera is likely derived.

Clarke *et al.* (1979) support the suggestion made by J. Young (1970) that the eye stalks of cranchiids may contain ammonium to provide buoyancy, but eye stalks may be of additional advantage to the larva by providing greater mobility to the eyes, thereby affording broader vision (J. Young, 1970; R. Young, 1975b; Weihs & Moser, 1981). The loss of the eye stalks with growth can be related to the vertical distribution of the animal (R. Young, 1975a,b). The length of time that the larvae spend in the shallower waters appears to correspond with the varying persistence of eye stalks in the different species, but does not necessarily correspond with the degree of development of the stalks.

Character 14. *Dorsal pad of funnel organ*:

- (a) one median papilla plus two lateral flaps;
- (b) one median flap plus two lateral flaps;
- (c) two lateral flaps;
- (d) one median papilla plus two to six markedly flattened, lateral papillae;
- (e) one median papilla plus two round or elliptical, lateral papillae;
- (f) two lateral papillae.

The funnel organ, comprised of one or more pads of mucus-secreting epithelium, is found on the inner surface of the funnel in all cephalopods. Usually located in the middle

part of the funnel, the organ is sometimes confined to the dorsal surface, as in nautiloids, some octopods, and *Vampyroteuthis*, or may be found on both the dorsal and ventral surfaces, as in the majority of cephalopods. In octopods, the organ is generally W-shaped, but the lateralmost of the vertical bars are sometimes separate, or the organ may take the form of two modified V-shaped pads. In sepoids and teuthoids, the funnel organ is typically three parted—an inverted V- or U-shaped dorsal pad and two paired, usually oval and elliptical-shaped, ventral pads. Variations in the size, outline and surface sculpture of these two basic forms of pads is considerable, especially among oegopsids. Variation is greater in some families than in others, and is displayed to the highest degree among cranchiids.

The sculpture of the dorsal member of the funnel organ has received the most taxonomic attention. In the Cranchiidae, the dorsal pad always has sculpture on the lateral arms. The pad may exhibit one median papilla plus two lateral flaps (*Sandalops*), one median flap plus two lateral flaps (*Cranchia* and *Lio-*

cranchia), two lateral flaps (*Egea* and *Megalocranchia*), one median papilla plus two to six markedly flattened, lateral papillae (*Leachia*), one median papilla plus two round or elliptical, lateral papillae (*Helicocranchia*, *Liguriella*, *Taonius*, *Galiteuthis*, *Mesonycho-teuthis* and *Teuthowenia*), or two lateral papillae (*Bathothauma*) (Fig. 7).

The lateral flaps that occur in *Sandalops*, *Cranchia*, *Liocranchia*, *Egea* and *Megalocranchia* are all longitudinally (i.e. antero-posteriorly) oriented. In *Leachia*, the flattened, lateral papillae are also longitudinally oriented, and when the lateral papillae are multiple on a side, they form along a single anteroposterior line and are sometimes connected by a basal ridge, all suggesting that the papillae have developed from a longitudinal flap. There is a trend in *Leachia* toward multiple lateral papillae; the number of papillae may vary within a species or an individual, where sometimes there is a single papilla on one side and two on the other. In the majority of the members of the outgroup, the dorsal pad is unsculptured except for a median papilla. Several members have a longitudinal ridge,

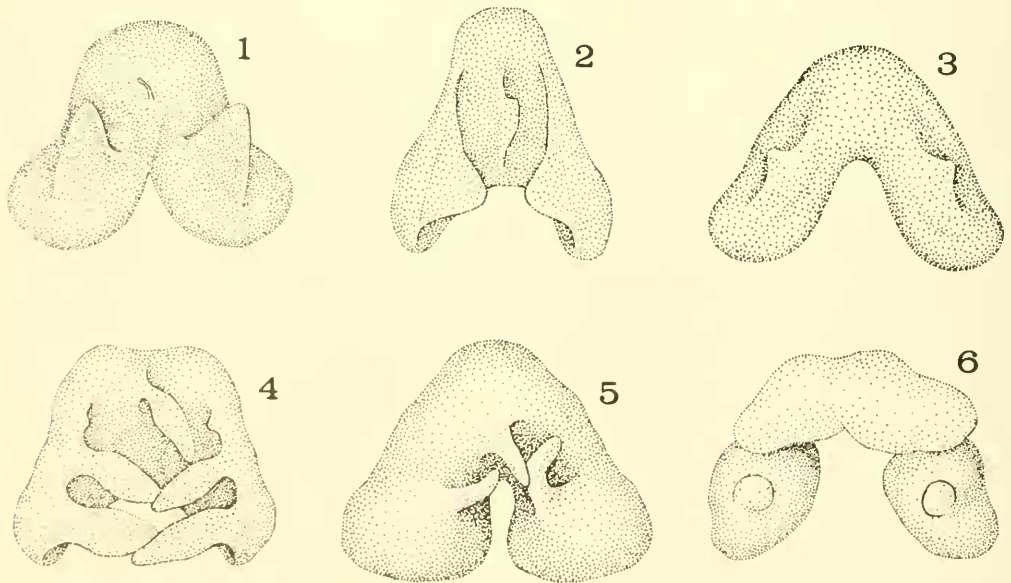


FIG. 7. Dorsal pad of funnel organ: (1) *Sandalops* sp. C, CI 71-6-26 (USNM), adult, 102 mm mantle length; (2) *Cranchia scabra*, WH 439-II-71 (ZMH), subadult, 122 mm mantle length; (3) *Egea inermis*, WH 471-II-71 (ZMH), subadult, 207 mm mantle length; (4) *Leachia danae*, MV 65-I-53 (SIO), subadult, 167 mm mantle length; (5) *Galiteuthis glacialis*, Elt 1323 (USNM), subadult, 333 mm mantle length; (6) *Bathothauma* sp. D, C 108662 (AM), subadult, 187 mm mantle length (1, 3 from N. Voss, 1980; 5 redrawn from McSweeney, 1978) (see Character 14).

developed to various extents, either on the lateral or median sections of the pad or on both.

The occurrence of a median papilla in the majority of the cranchiids, and of a longitudinally oriented flap, or its apparent modifications, on each lateral arm in nearly half of the family, is similar to the occurrence in the outgroup of a median papilla in most of the members, and of a longitudinal ridge on the lateral arm when lateral sculpture is present. This suggests that a dorsal pad with one median papilla and two lateral flaps as found now only in *Sandalops*, might be considered primitive to the cranchiids. The remaining character states appear to be independently derived except for "(f) two lateral papillae," which is hypothesized to have been derived from "(e) one median papilla plus two round or elliptical, lateral papillae." Nesis (1974), in his analysis of the sculpture of the dorsal pad in the Taoniinae, concluded that the state "one median papilla and two lateral papillae" was basic to the subfamily and that the flaps were derived. His conclusions resulted from analysis of the distribution of character states only in the taoniins, however; he did not study the

family as a whole nor compare the character as it occurs in other families considered to be allied. Our conclusions appear supported by a broader comparative approach.

Though the function of the funnel organ and the significance of its variations are not known, it has been considered that the mucus produced is used for keeping the funnel and perhaps mantle cavity clean of debris. An alternate or additional function is suggested by the observations of Hall (1956), Nicol (1964) and M. R. Clarke (as reported by Dilly & Nixon, 1976) that the mucus might serve as a carrier for the ink produced by the ink sac and expelled through the funnel by the animal when irritated.

2. A Phylogenetic Hypothesis

Application of the Wagner method to the binary data matrix of Table 2 yields the reconstruction of cranchiid evolutionary history illustrated in Fig. 8. In Fig. 8, internal nodes (branching points) represent hypothetical ancestors and are labelled with capital letters; external nodes (branch tips) represent extant cranchiids and are labelled with the first three

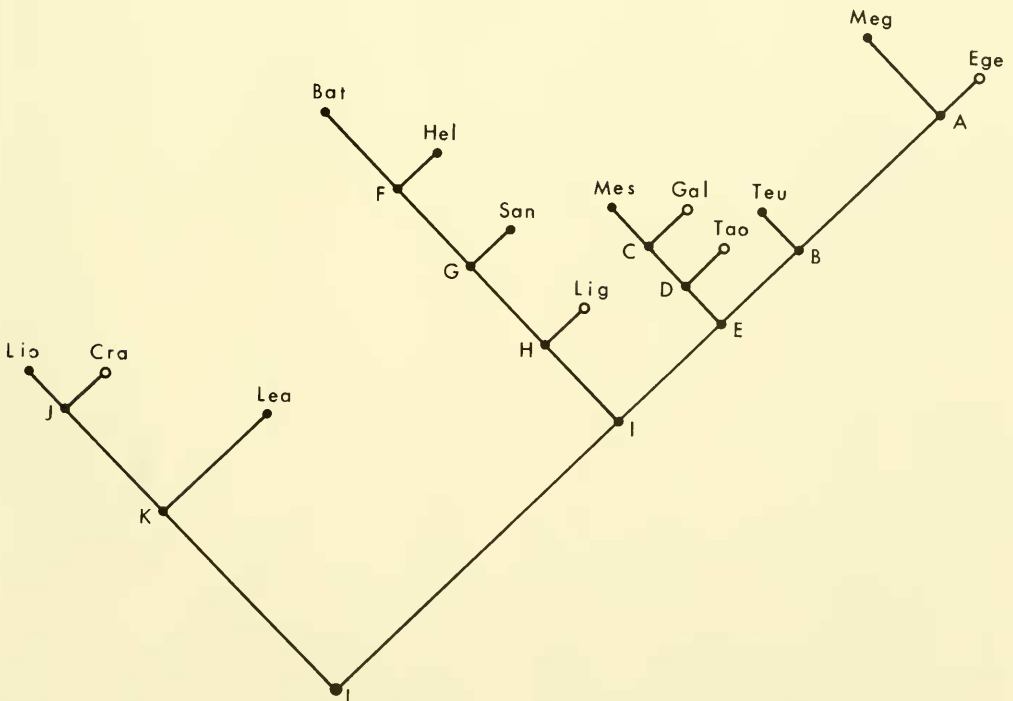


FIG. 8. Wagner reconstruction of cranchiid phylogeny. See text for explanation.

letters of the generic name; lines connecting the nodes represent phyletic lineages and are drawn proportional to the estimated amounts of morphological evolution (number of character state transitions) that separate extant cranchiids from their hypothetical ancestors or hypothetical ancestors from one another. Some extant cranchiids are indistinguishable from their most recent shared ancestors with respect to the characters employed in this study; the external nodes representing these forms (e.g., *Liguriella*) are drawn as open circles and have been removed an arbitrary one branch length unit from their most recent ancestors. Phenotypes of hypothetical ancestors are provided in Table 3.

The Wagner Tree hypothesizes a basal separation of the Cranchiidae into two phyletic lineages that correspond in membership to the traditional subfamilies Cranchiinae and Taoniinae, the Cranchiinae containing *Cranchia*, *Liocranchia* and *Leachia*, and the Taoniinae comprised by the remaining ten genera. Within the taoniin clade, three major generic assemblages can be discerned, two of which, the group *Megalocranchia* + *Egea* + *Teuthowenia* and the group *Taonius* + *Galiteuthis* + *Mesonychoteuthis*, are further hypothesized to have shared a common ancestor more recently than either did with members of a third group consisting of *Sandalops* + *Liguriella* + *Helicocranchia* + *Bathothauma*. All relationships are fully resolved in this estimate of cranchiid phylogeny, and the topology of the tree requires a minimum of 45 character state transitions in order to derive observed phenotypes of extant cranchiids from the morphology of the common ancestor estimated in the preceding section; the consistency index (Kluge & Farris, 1969) for the Wagner Tree is .69, indicating a remarkably good fit of hypothesis to data.

Because it cannot be known with certainty, however, that the Wagner Tree is actually the most parsimonious of all possible reconstructions of cranchiid relationships, the binary data matrix of Table 2 was subjected to Compatibility Analysis in order to develop testable alternatives. The 31 binary factors of our data form 21 cliques of mutually compatible members, and each of these cliques supports one (or more) estimate(s) of cranchiid evolution that is (are) not supported by any other clique. The compatibility matrix for the binary factors is presented in Table 4, character memberships of the ten largest cliques are provided in

TABLE 3. Reconstructed phenotypes of hypothetical cranchiid ancestors. Columns represent the hypothetical ancestors labelled with capital letters in Fig. 8. Character numbers and character state labels are the same as those in Table 1 and described in the text.

Character number	Ancestors											
	A	B	C	D	E	F	G	H	I	J	K	L
1	b	a	a	a	a	c	c	a	a	d	d	a
2	c	c	c	c	c	a	a	b	b	a	a	a
3	c	c	b	b	b	d	a	a	a	a	a	a
4	a	a	a	a	a	a	a	a	a	b	b	a
5	a	b	b	b	b	b	b	b	b	a	a	a
6	e	e	e	e	e	c	d	d	d	b	b	a
7	b	b	b	b	b	b	b	b	b	a	a	a
8	b	b	a	a	a	a	a	a	a	b	b	a
9	a	a	c	b	a	a	a	a	a	a	a	a
10	a	a	a	a	a	b	b	b	a	a	a	a
11	b	b	b	b	b	c	c	c	b	c	a	a
12	a	a	a	a	a	a	a	a	a	b	b	a
13	b	b	b	b	b	b	b	b	b	a	a	a
14	c	e	e	e	e	e	e	e	e	e	b	a

Table 5, and the cladograms supported by the two largest cliques are drawn in Fig. 9.

Cliques I and II, whose trees are drawn in Fig. 9, share 21 binary factors (1b, 1d, 2c, 2d, 3b, 3c, 3d, 4b, 6b, 6c, 6e, 6f, 7b, 9b, 9c, 10c, 12b, 14b, 14c, 14d, 14f), and this large set of characters determines those cladistic patterns common to both compatibility trees and to the results of Wagner analysis. Disagreement between the two trees of Fig. 9 reflects underlying differences in clique memberships and concerns only the relationships of *Sandalops* and *Liguriella* within the Taoniinae. Clique I differs from clique II by the inclusion of binary factor 1c which asserts that *Bathothauma*, *Helicocranchia* and *Sandalops* comprise a monophyletic group, but leaves the relationships of *Liguriella* unresolved. Clique II omits factor 1c but includes factor 6d whose effect is to remove *Sandalops* and *Liguriella*, but not *Helicocranchia* or *Bathothauma*, to a monophyletic group with the remaining six taoniin genera; the relationships of *Sandalops* and *Liguriella* within the latter group are unresolved, however.

The trees supported by cliques I and II both include trichotomies because binary characters that might fully resolve the relationships of *Liguriella* and/or *Sandalops* do not support other aspects of the cladograms drawn in Fig. 9. In order to test the compatibility results

TABLE 4. Compatibility matrix for the binary factors whose distributions are provided in Table 2. Because the matrix is symmetrical, only the lower half is illustrated. Rows and columns are binary factors; an entry of (0) for a given row and column signifies that the corresponding pair of binary factors is not compatible, an entry of (1) that the pair of factors is compatible.

Binary factor label	1b	1c	1d	2b	2c	2d	3b	3c	3d	4b	5b	6b	6c	6d	6e	6f	7b	8b	9b	9c	10b	10c	11b	11c	12b	13b	14b	14c	14d	14e	14f
1c	1																														
1d	1	1																													
2b	1	1	0																												
2c	1	1	1	1																											
2d	1	1	1	1	1																										
3b	1	1	1	1	1	1																									
3c	1	1	1	1	1	1	1																								
3d	1	1	1	1	1	1	1	1																							
4b	1	1	1	0	1	1	1	1	1																						
5b	1	1	0	0	0	1	0	0	1	0																					
6b	1	1	1	0	1	1	1	1	1	1	1																				
6c	1	1	1	0	1	1	1	1	1	1	0	1																			
6d	1	0	1	0	1	1	1	1	1	1	0	1	1																		
6e	1	1	1	1	1	1	1	1	1	1	0	1	1	1																	
6f	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1																
7b	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1															
8b	1	1	1	0	0	1	0	1	1	1	0	1	0	0	0	1	0														
9b	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1													
9c	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1												
10b	1	0	1	0	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1											
10c	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1										
11b	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1							
11c	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1							
12b	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0							
13b	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0					
14b	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
14c	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
14d	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
14e	1	0	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1	1	1	1	1
14f	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

TABLE 5. Memberships for the ten largest cliques of mutually compatible binary factors.

Clique number	Membership
I	1b, 1c, 1d, 2c, 2d, 3b, 3c, 3d, 4b, 6b, 6c, 6e, 6f, 7b, 9b, 9c, 10c, 12b, 14b, 14c, 14d, 14f.
II	1b, 1d, 2c, 2d, 3b, 3c, 3d, 4b, 6b, 6c, 6d, 6e, 6f, 7b, 9b, 9c, 10c, 12b, 14b, 14c, 14d, 14f.
III	1b, 1d, 2c, 2d, 3b, 3c, 4b, 6b, 6c, 6e, 6f, 7b, 9b, 9c, 10b, 10c, 12b, 14b, 14c, 14d, 14f.
IV	1b, 1c, 2c, 2d, 3b, 3c, 3d, 6c, 6e, 6f, 7b, 9b, 9c, 10c, 13b, 14b, 14c, 14d, 14f.
V	1b, 2c, 2d, 3b, 3c, 3d, 6c, 6d, 6e, 6f, 7b, 9b, 9c, 10c, 13b, 14b, 14c, 14d, 14f.
VI	1b, 1d, 2d, 3d, 4b, 6b, 6c, 6f, 7b, 9b, 9c, 10c, 12b, 14b, 14c, 14d, 14e, 14f.
VII	1b, 1c, 1d, 2d, 3c, 3d, 4b, 6b, 6f, 8b, 9b, 9c, 10c, 12b, 14b, 14c, 14d, 14f.
VIII	1b, 2c, 2d, 3b, 3c, 6c, 6e, 6f, 7b, 9b, 9c, 10b, 10c, 13b, 14b, 14c, 14d, 14f.
IX	1b, 1d, 2d, 3c, 4b, 6b, 6f, 8b, 9b, 9c, 10b, 10c, 12b, 14b, 14c, 14d, 14f.
X	1b, 1c, 2b, 2c, 2d, 3b, 3c, 3d, 6e, 6f, 9b, 9c, 10c, 14c, 14d, 14f.

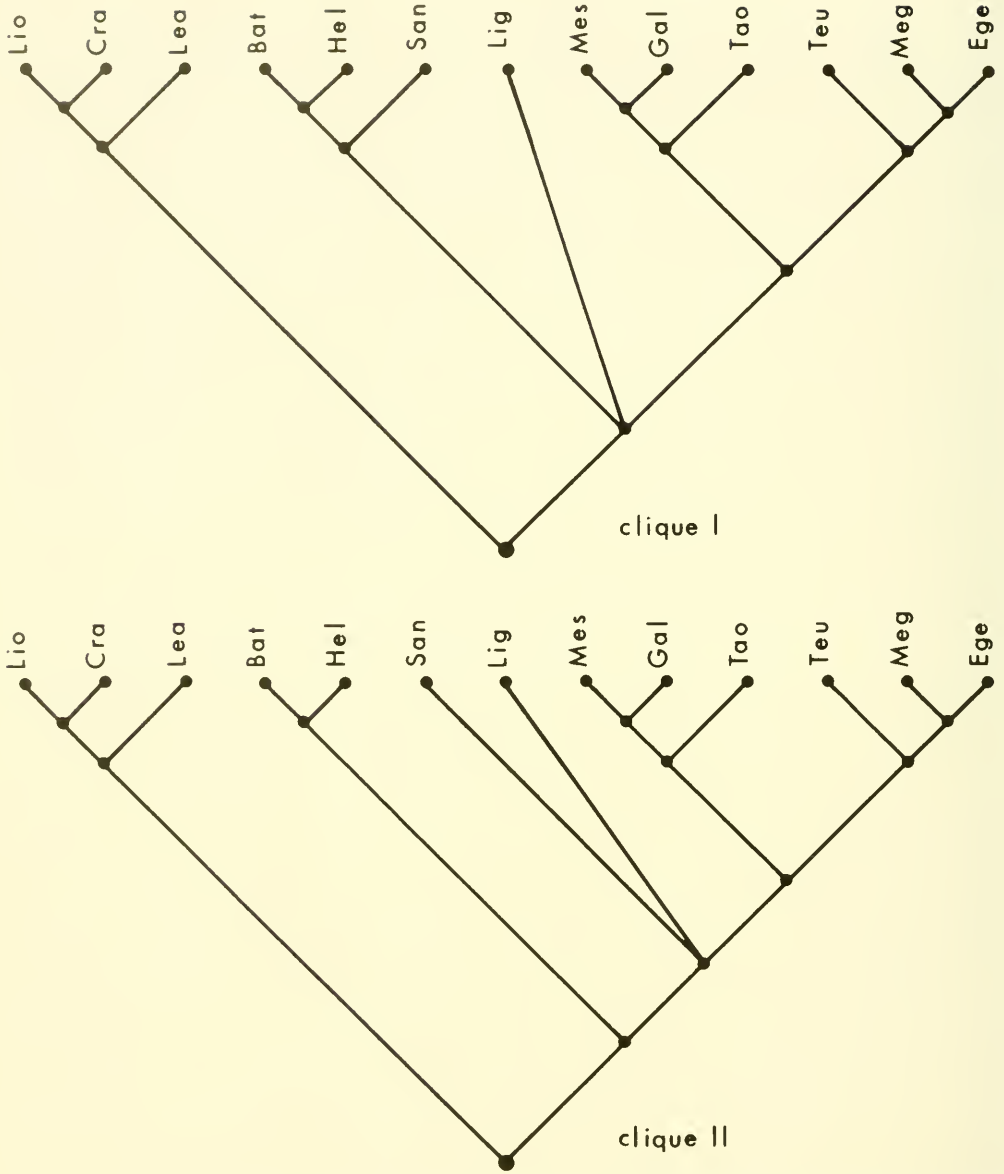


FIG. 9. Cladograms corresponding to the estimates of cranchiid evolution supported by cliques I and II (see Table 5). Branch lengths are arbitrary and do not represent any estimated parameter of phylogeny.

against those of the Wagner analysis, however, it is convenient to resolve such trichotomies fully. To each trichotomy in a cladogram there correspond three completely bifurcating alternative interpretations (Nelson & Platnick, 1980), and the six alternatives that result from so interpreting the ambiguities of Fig. 9 are shown in Fig. 10. Only that por-

tion of the taoniin lineage descended from the cranchiid ancestor but ancestral to the monophyletic group *Megalocranchia* + *Egea* + *Teuthowenia* + *Taonius* + *Galiteuthis* + *Mesonychoteuthis* is depicted for each variant; the unillustrated portions of the cladograms of Fig. 10 are identical to those elicited in all preceding analyses. We note that one of

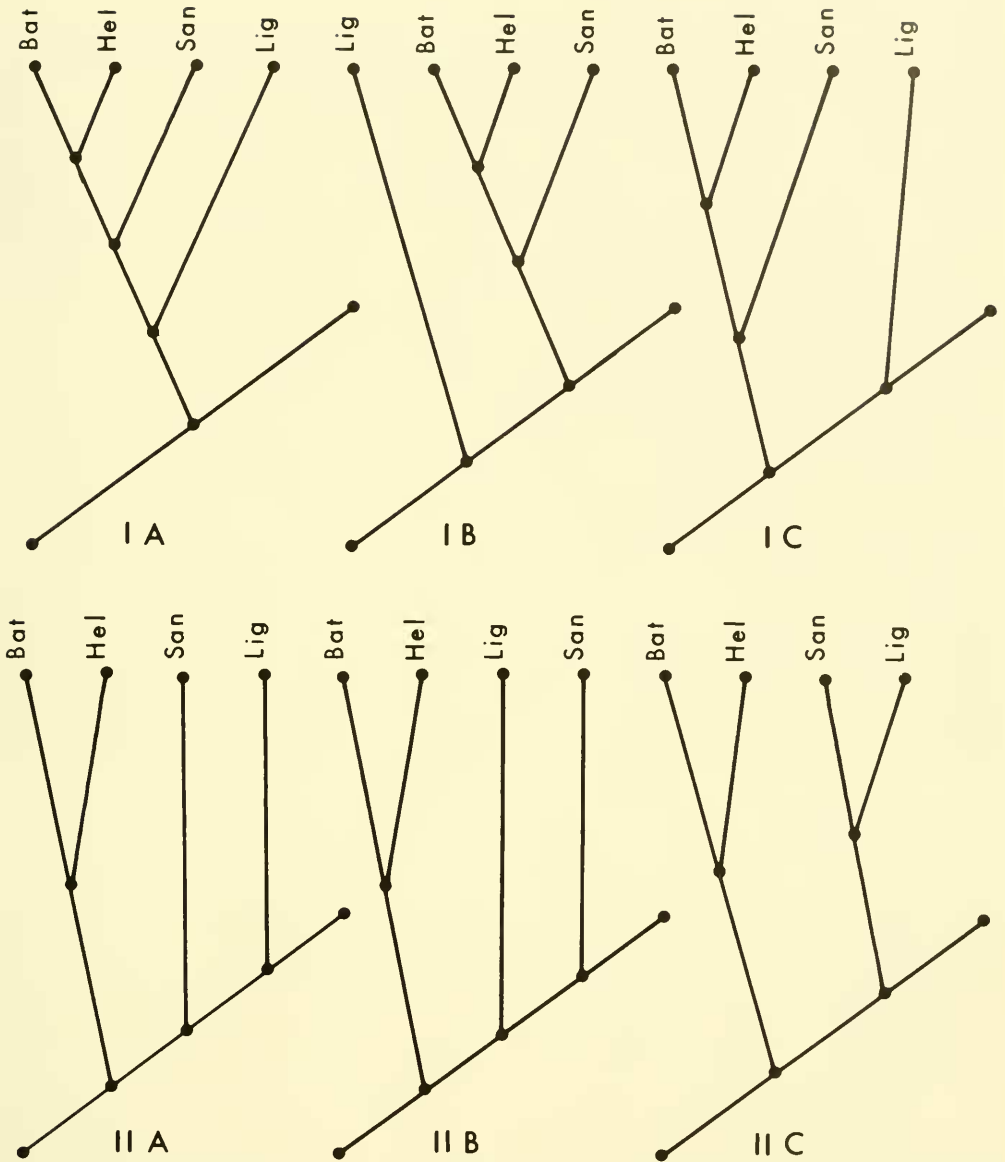


FIG. 10. Three bifurcating interpretations for each of the trichotomous branchings in the cladograms of Fig. 9. See text for explanation.

the bifurcating interpretations of the tree determined by clique I is identical with the Wagner Tree.

A modified version (see Materials and Methods) of the parsimony-optimizing procedure of Farris (1970) was used to fit observed character state distributions (Table 1) to the six variants in order to determine which

of them provides the most parsimonious interpretation of cranchiid phylogeny. The Wagner Tree (Fig. 8 and 1A of Fig. 10) with 45 required character state transitions proved most parsimonious, followed by trees IC, IIA and IIC with 46 necessary transitions apiece, and trees IB and IIB with 47 transitions each. The character state transition in which two of

these hypotheses differ are illustrated in Fig. 11. As can be seen, while both hypotheses 'explain' the same observed phenotypes for the four genera diagrammed, they differ in the simplicity with which they do so.

DISCUSSION

In the absence of fossil cranchiids and of a *priori* knowledge of character conservatism among these squids, the principle of parsimony appears to us the only defensible criterion with which to test alternative hypotheses of cranchiid phylogeny. However, because more than 300 billion different bifurcating tree diagrams could be drawn to unite our 13 terminal taxa (Felsenstein, 1978) exhaustive testing by any criterion is clearly impractical. The purpose of applying operational phylogenetic techniques, as those employed here, is simply to reduce this vast array of possibles to a much smaller set of well-corroborated alternatives among which the true phylogeny has a reasonably high likelihood of being included. The close congruence revealed above between the results of Wagner and of Character Compatibility analyses lends credence to the possibility that the tree diagram

of Fig. 8 represents, if not historical truth exactly, then at least an estimate sufficiently close that an examination of the details of the reconstruction will not be far wrong. Although Pfeffer (1912) and Nesis (1974) previously discussed phylogenetic relationships among cranchiids, the inadequate materials available to them resulted in such taxonomic confusion as to effectively preclude meaningful comparisons of their conclusions with our results; the reader is referred to N. Voss (1980) for a discussion of their generic assignments.

A basal division of the Cranchiidae into the traditional subfamilies Cranchiinae and Taoniinae is supported by five characters (1, 4, 6, 7, 12), and character state transitions separating the cranchiian and taoniin ancestors (Table 3) account for nearly 30% of all of the morphological evolution estimated to have occurred in the course of cranchiid phylogeny. Apparently unique synapomorphies uniting the three cranchiian genera are the cartilaginous strengthenings along one or both of the paired ventral lines of funnel-mantle fusion (1d), the lateral fusion of the funnel to the head (4b), the possession of four or more small and simple ocular photophores (6b) and of a caecum larger than the stomach (12b). Unique synapomorphies to support a hy-

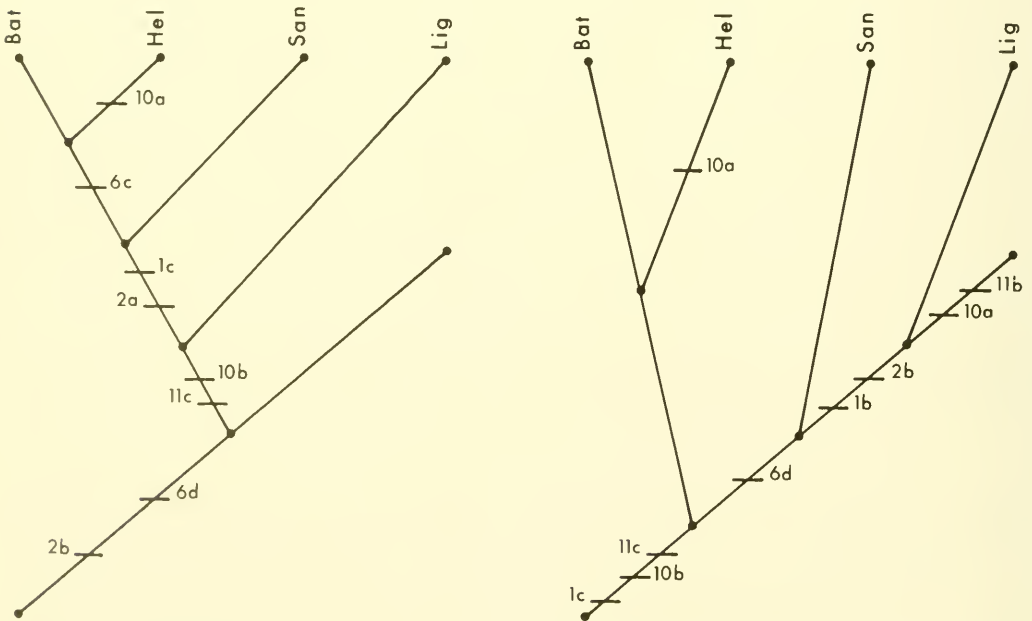


FIG. 11. Two alternative estimates of relationships for four cranchiid genera. The labelled slashes across branches of the tree signify the evolution of the corresponding character state from a locally more plesiomorphic condition. Only those character state transitions in which the two hypotheses differ are illustrated.

pothesis of taoniin monophyly are the loss of the hectocotylus (7b) and the possession of ocular photophores of complex construction (6c-f). Other derived conditions that may have characterized the cranchiid or taoniin ancestor are the results of non-unique character state transitions (i.e. those replicated or reversed elsewhere) that do not, therefore, support the cranchiid-taoniin dichotomy *per se*.

Within the Cranchiinae, the genera *Cranchia* and *Liocranchia* form a monophyletic group that is supported by a derived morphology of the funnel organ (14b) as well as by the position of the digestive duct appendages on the digestive gland alone (11c); the latter state, however, is shared with some taoniin genera as well (see below). *Leachia* appears well separated from the other two cranchiids in the characters discussed above and in the morphology of funnel-mantle fusion (see discussion of Character 1) and shares with the Taoniinae the derived absence of a funnel valve (5b; except *Egea* and *Megalocranchia*) and the presence of stalked larval eyes (13b). These last two anomalous traits may either represent convergent evolution of the derived conditions in question, or we may be mistaken in assuming sessile larval eyes and the presence of a funnel valve to be primitive for the family. If it is our estimation of polarities that is in error, then a funnel valve and sessile larval eyes are synapomorphies for *Cranchia* and *Liocranchia*.

The major monophyletic clusters identifiable within the Taoniinae include the generic groups recognized by N. Voss (1980), but substantial refinements of earlier hypotheses of taoniin interrelationships are also represented in Fig. 8. The *Megalocranchia* group (*Megalocranchia* + *Egea* + *Teuthowenia*) and the *Taonius* group (*Taonius* + *Galiteuthis* + *Mesonychoteuthis*) together comprise a monophyletic unit defined by shared, derived aspects of gladius morphology (2c), fin shape (3b,c) and ocular photophore arrangement (6e,f) that appears well separated from its putative (see below) sister group, the *Sandalops* assemblage (*Sandalops* + *Liguriella* + *Bathothauma* + *Helicocranchia*).

Monophyly of the *Megalocranchia* group is supported by shared possession of elongated, terminal-lateral fins (3c) and by the presence of brachial end-organs on the arms of mature females (8b). Brachial end-organs, however, also occur among cranchiid squids and seem best regarded as another instance of convergent evolution. To argue otherwise,

for example that cranchiids and the *Megalocranchia* group form a monophyletic assemblage by virtue of a unique derivation of brachial end-organs, would necessarily invoke homoplasy in so many other characters (e.g. 2, 3, 6, 7) as to be extravagantly unparsimonious. Within the *Megalocranchia* group the genera *Megalocranchia* and *Egea* form a morphologically distinctive pair as noted by N. Voss (1980: 406).

Members of the *Taonius* group uniquely share the derived presence of hooks or of hooklike teeth on the larger suckers of the clubs (9b,c). *Taonius*, *Galiteuthis* and *Mesonychoteuthis* are also united by having lanceolate or stout, ovate, terminal fins (3b), a character state derived for the Taoniinae as a whole but a plesiomorph within the monophyletic assemblage that includes *Megalocranchia* and its allies. *Mesonychoteuthis* and *Galiteuthis* both exhibit clubs with well-developed hooks (9c), a uniquely derived condition not shared with *Taonius*. Four species of *Galiteuthis* share, with *Mesonychoteuthis*, the (not uniquely) derived position of digestive duct appendages on the digestive gland alone (11c), but two other species of *Galiteuthis* share with *Taonius* the more plesiomorphic position of appendages on both the gland and the digestive ducts (11b). All of the analyses reported here were repeated, using either 11b or 11c to characterize *Galiteuthis*, with identical results: the cladistic position of the genus was unaffected by the substitution. The distinctiveness of neither *Mesonychoteuthis* nor *Galiteuthis* is compromised by the interspecific variation in Character 11 observed within the latter; the two genera are well defined with respect to other morphological features discussed by N. Voss (1980: 392-396).

All of the relationships discussed above are common to the results of both Wagner and Character Compatibility analyses and appear adequately supported by the comparative morphological evidence at our disposal. Regrettably, the same cannot be said of any arrangement of the genera *Bathothauma*, *Helicocranchia*, *Sandalops* and *Liguriella* along the phyletic line descended from the cranchiid ancestor but ancestral to the *Taonius* and *Megalocranchia* groups. While the hypothesis that the four genera of the *Sandalops* assemblage form a monophyletic cluster is slightly more sparing of character state transitions than any of the other five alternatives treated here (Fig. 10), we would

point out that no unique synapomorphy can be adduced in support of this arrangement. Instead, members of the *Sandalops* group are united by character states that are shared by other cranchiids as well (4a, 5b, 7b, 8a, 9a, 11c, 12a, 13b) and evidence for their near affinity is therefore largely by phenetic similarity.

By contrast, derived resemblances in ocular photophores (6d and derivatives) argue that *Sandalops* and *Liguriella* form a monophyletic unit with the *Taonius* and *Megalocranchia* groups that does not include *Bathothauma* or *Helicocranchia* (tree II of Fig. 9) while the shared, derived possession of narrow, straight funnel-mantle fusion cartilages supports the inclusion of *Bathothauma*, *Helicocranchia* and *Sandalops*, but not *Liguriella*, in a different monophyletic arrangement (tree I of Fig. 9). The most parsimonious arrangement (Fig. 8 and IA of Fig. 10) is supported weakly by assuming the presence of digestive duct appendages on the digestive gland alone (11c) to be a local synapomorphy; the condition is shared with *Mesonychoteuthis*, one group of *Galiteuthis* species, *Cranchia* and *Liocranchia*, however, and the hypothesis that the *Sandalops* assemblage is monophyletic should be regarded as a best guess among alternatives but slightly less parsimonious; only the discovery of new characters seems likely to satisfactorily resolve the phyletic structure of this problem group. *Bathothauma* and *Helicocranchia* share morphologies of the fins (3d) and ocular photophores (6c) that are unique among adult cranchiids though widespread in the larval stages of other genera; as adult features of *Bathothauma* and *Helicocranchia*, the traits appear to represent derived, neotenous conditions.

Cranchiid adaptive radiation appears to have involved, to a significant degree, the evolution of differing schedules of ontogenetic descent in the water column (N. Voss, unpublished notes), and several of the monophyletic groups discussed in the preceding paragraphs may be characterized by the ecological distribution of the growth stages of their member taxa. Thus, the three cranchiid genera on the one hand and the genera of the *Megalocranchia* group on the other represent apparently independent clades whose larvae (with the single known exception of *Liocranchia valdiviae*) nevertheless resemble one another ecologically by remaining in the upper waters for longer periods in their devel-

opment than do larvae of other cranchiid groups. This ecological resemblance, either convergently evolved or inherited unmodified from the cranchiid ancestor, might account for the peculiar similarities between the groups in possession of brachial end-organs and (between *Liocranchia-Cranchia* and *Egea-Megalocranchia*) in the presence of a valve in the funnel. However, as we know so little of the adaptive significance of either anatomical trait, their causal relationships (if any) to ontogenetic lingering in the upper waters are unclear.

The *Taonius* group, in contrast, consists of cranchiids that typically descend to mid and deep water at a much earlier immature stage than do members of the Cranchiinae or of the *Megalocranchia* group. It may be noted in passing that the phenomena of early ontogenetic descent displayed by the *Taonius* group might be related to the extended geographic distribution of the member genera. Though circumglobal distribution in tropical and subtropical waters is typical for most of the cranchiid genera, the ranges of the *Taonius* assemblage extend into subpolar and polar regions, with *Mesonychoteuthis* restricted primarily to Antarctic waters. Geographic range extension into cold waters is not unique to this group, however, for *Teuthowenia*, and, to a lesser extent, *Liguriella* and *Bathothauma* are also found in subpolar waters, but in a more limited pattern of distribution.

The *Sandalops* group is not easily defined in ecological terms and the lack of morphological cohesiveness remarked earlier for these squids may be a reflection of the apparent absence of any ecological distinctiveness.

Functional correlations appear to have contributed little, if at all, to the hierarchic pattern of character state distributions revealed in the preceding analyses: the phylogeny is supported by morphological features associated with such a diversity of biological activities (see discussions of Characters 1, 3, 4, 7, 9, 12) that we think it unlikely that our estimate of relationships reflects divergence in only a single co-adapted anatomical complex or functional role. Of the characters treated here, only two seem obviously associated in a close functional sense: the form of the posterior end of the gladius (Character 2) and the shape of the fins (Character 3). As discussed previously in the analyses of these characters, changes in the shape of the posterior end of the gladius are usually accompanied by changes of fin

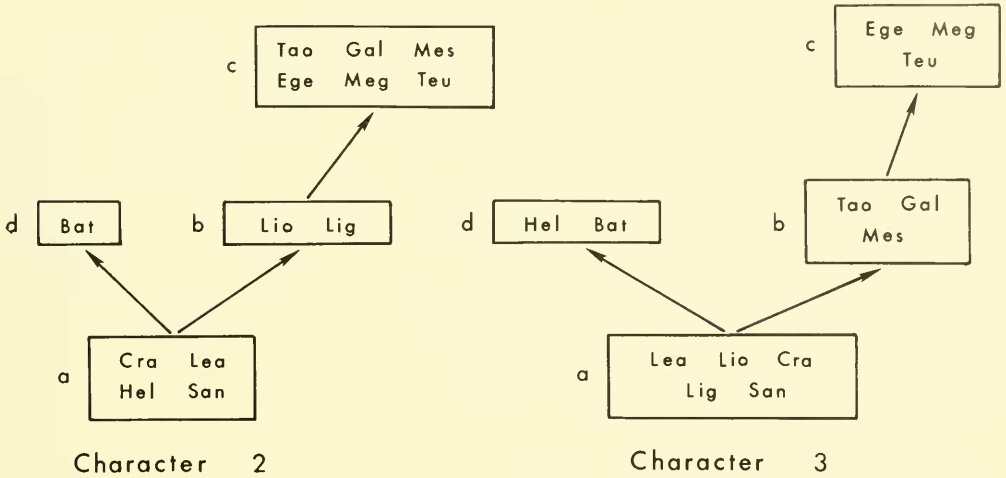


FIG. 12. Enlarged tree diagrams for Characters 2 and 3. Lower case letters label the states of Characters 2 and 3, drawn as boxes containing the cranchiid genera that exhibit the appropriate morphological condition; arrows indicate polarities hypothesized in the text. The two characters are seen to constitute different (but compatible) partial estimates of cranchiid relationships.

shape, perhaps for reasons of structural support. Nevertheless, as can be seen from the enlarged character state trees in Fig. 12, the relationship between fins and gladius is evidently not wholly deterministic, and the two characters each contribute some phyletic information not contained in the other. We observe that Character 2 does not, in fact, support our hypothesis of phylogeny while Character 3 does.

The fact that not all of the characters we studied are pairwise compatible (Table 4) is sufficient demonstration of the existence of homoplasy in the course of cranchiid evolution. If the tree topology of Fig. 8 and the reconstructed ancestral phenotypes of Table 3 be accepted as reasonable estimations, then the minimal amount of homoplasy in each character commensurable with those estimates is easily determined and may provide an approximate measure of conservatism that might inform the choice and weighting of characters in subsequent systematic studies (see also Farris, 1969).

Characters 1, 3, 4, 7, 9, and 12 support the estimate of Fig. 8; if that estimate is taken to be correct, then these characters, in addition to being mutually compatible, are also true characters: they have undergone no homoplasy in the course of cranchiid evolution. Characters 2, 5, 6, 8, 10, 11, 13 and 14 have all undergone one or more instances of convergence or reversal, of which those involving brachial end-organs (Character 8), larval eye

position (13) and a funnel valve (5) have already been discussed as examples above. Most of these latter characters have undergone but one or two instances of homoplasy, and we would hesitate, based on this observation alone, to enjoin caution in their use in future phylogenetic investigations, but Character 11 is an exception. Over the course of cranchiid phylogeny, digestive duct appendages appear to have migrated on and off the digestive duct and gland with abandon. Primitively situated on the digestive duct (see analysis for Character 11, above), appendages are here interpreted to have moved onto the digestive gland in the common ancestor of *Cranchia* and *Liocranchia*, and in the taoniin ancestor, to have reverted to the ancestral state in *Megalocranchia*, and to have vanished from the ducts entirely in *Cranchia* and *Liocranchia*, in the ancestor of the *Sandalops* group and in *Mesonychoteuthis* and some species of *Galiteuthis*. Evidently, the digestive duct appendages are evolutionarily labile structures, and it would be interesting to know what adaptive significance accruing to their anatomical positions makes them so.

CONCLUDING REMARKS

The form of a phylogenetic hypothesis, the topology of a tree diagram, results both from the analysis of individual characters and from the procedures subsequently employed to re-

solve character conflicts. We have endeavored to be as explicit as possible about each step that led us to adopt the hypothesis presented here so that would-be critics can discover exactly where we may have gone wrong and set about directly to correct the error. Because errors in phylogeny reconstruction, when they exist, usually consist of mistakes in determining homologies or in estimating polarities, the greater part of this paper is devoted to individual character discussions, and the future, critical tests of our phylogeny that we hope to have provoked will perforce consist either of discovering new characters or of more detailed analyses of the characters treated here. In neither case will materials be found wanting. As sources of new characters, for example, the myology of teuthoids remains little explored; the morphology of the cranial cartilages and the spermatophores likewise invites attention as does the comparative anatomy of the nervous, reproductive and circulatory systems. Of characters treated here, the histology of the ocular photophores and of the brachial end-organs is in need of study, and careful observations of courtship and mating behavior may confidently be expected to permit more informed treatment of the hectocotylus and of other male sexual modifications of the arms. Additionally, we know little or nothing of the functional significance of variations in the form of the funnel organ, of the larval eye stalks, or of the relative size of the caecum and stomach to name but three of many enigmatic aspects of cranchiid morphological variation. References provided in the individual character discussions will provide introductions to these and other promising areas of teuthoid morphological research; we know of few animal groups in which the potential for innovative and phylogenetically rewarding comparative studies appears so great.

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